AN ANALYSIS OF LATE PLEISTOCENE HOMININ POPULATION DYNAMICS IN EUROPE USING ECOLOGICAL NICHE MODELING METHODS

A Dissertation

by

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ABSTRACT

This dissertation addresses questions concerning the patterns of population dynamics between Late Neandertals and early modern humans (EMHs) during the Late Pleistocene of Europe and the fluctuation of those patterns over time. Proposed models of Neandertal extinction and EMH expansion hypothesize certain patterns of behavioral responses to fluctuating climate and possible biogeographic features, such as the hypothesized Ebro River Frontier (EFM). Analyses designed to illuminate these potential patterns and test the presence of proposed biogeographic frontiers were conducted using the Genetic Algorithm for Rule-Set Prediction (GARP), originally designed for ecological research to model the geographic extent of suitable habitat associated with samples of presence-points and make well-informed hypotheses about the fundamental niche parameters of a species.

Three different paleoenvironmental reconstructions that shortly precede Neandertal extinction were used in this study to model the possible change in these patterns over time centered on Heinrich Event 4 (H4): 1) the Pre-H4 (43.3-40.2 ky cal BP), 2) the H4 (40.2-38.6 ky cal BP), and 3) the Post-H4 (38.6-36.5 ky cal BP). For the time period of each reconstruction, multiple experiments were run with different samples of locations absolutely dated to each time period designed to capture Neandertal and EMH presence. These samples move from more theoretically conservative groups of morphologically diagnostic fossil hominin remains to those which included Middle Paleolithic (MP) and Upper Paleolithic (UP) sites. The resulting consensus prediction

models were statistically validated with a combination of Pearson's *p*-value, cumulative binomial probabilities, and Partial-ROC analyses.

The results of this dissertation indicated that Neandertals and EMHs display different behavioral responses to the H4. Neandertal suitable habitat contracts during the H4 and is thereafter confined to southern Europe. The total area predicted for Neandertals does not reach its Pre-H4 levels again. EMH suitable habitat does not show the same southern confinement. The total area predicted for EMHs remains steady throughout the H4, a short glacial period, and increases during the Post-H4. The geographic overlap for Neandertal and EMH suitable habitat is the most extensive during the Pre-H4. Despite similar niches, Neandertals and EMHs display different behavioral responses to climatic fluctuations.

DEDICATION

This dissertation is dedicated to my parents, Gary Gill Bible, PhD, and Tamia Jo Cloud Bible, CPA. Without your love and support, none of this would have been possible.

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NOMENCLATURE

AES	Afro-European Sapiens model
AHR	African Hybridization and Replacement model
AM	Assimilation Model
AMHs	Anatomically modern humans
BP	Before present
C&E	Center and edge model
CAS	Cohesive Adaptive Systems
ECNM	Eco-cultural niche modeling
EFM	Ebro Frontier Model
EMHs	Early modern humans
ENM	Ecological niche modeling
ESR	Electron spin resonance dating
GARP	Genetic Algorithm for Rule-Set Prediction
GIS	Geographic Information Systems
GUI	Graphical User Interface
H4	Heinrich Event 4
ky cal BP	Thousand calendar years before present
LGM	Last Glacial Maximum
LPT	Lowest presence threshold procedures
MP	Middle Paleolithic

MRE	Multiregional Evolution model
OOA	Out of Africa model
OS	Operating System
Pre-H4	Pre-Heinrich Event 4
Post-H4	Post-Heinrich Event 4
RAO	Recent African Origin model
SDMs	Species distribution models
THC	Thermohaline circulation
TL	Thermoluminescence dating
UP	Upper Paleolithic
U/TH	Uranium/thorium dating
WGS84	World Geodetic System 1984

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1. INTRODUCTION

Since the 1856 discovery of the first Neandertal specimen at Kleine Feldhofer Grotte, in the Neander Valley of Germany, anthropologists have been interested in answering the question of Neandertal taxonomic identity and whether or not Neandertals and modern humans were separated at the species or subspecific level (Trinkaus 1986; Trinkaus and Shipman 1993). This question is part of the debate surrounding the possible contribution of Neandertal genetic material to contemporary Early Modern Human (EMH) populations and the forces driving Neandertal extinction. Research questions regarding the Late Pleistocene of Europe have typically been framed from the perspective of modern human origins and the genetic makeup of contemporary humans. This results in studies that focus more on the purity of anatomically modern humans (AMHs), rather than examining the population dynamics of these two groups in Europe at a time of great environmental fluctuation and change (Trinkaus 2005). This dissertation is intended to investigate the patterning of these population dynamics using ecological niche modeling, a method novel to paleoanthropological research.

Modern models of Late Pleistocene evolution have a long history in paleoanthropological research and have inherited much from research conducted from the early 1900s onward. Two diametrically opposed models appeared very early in the academic literature with work by scientists such as Marcellin Boule and Ales Hrdlička: the Presapiens model and the Neandertal Phase model (Boule 1913; Boule 1921; Hrdlička 1927; Spencer and Smith 1981; Trinkaus and Shipman 1993). The Presapiens

model, which stated that Neandertals were an extinct side-branch of human evolutionary history, became one of the most influential evolutionary models in paleoanthropology and its echoes are still seen in modern research. The Neandertal Phase model instead concluded that modern Europeans had evolved solely and directly from Neandertals. While this conclusion has since been disproven (Aiello 1993; Spencer and Smith 1981; Trinkaus 2005; Trinkaus 2007; Trinkaus 2011; Trinkaus and Shipman 1993), this evolutionary model also had a great impact on later paleoanthropological research.

These two theoretical camps are distinguished by the weight that they place on the perceived importance of Neandertals in the processes of Late Pleistocene hominin evolution and the emergence of modern humans. The Presapiens model states that Neandertals had no impact on later hominin evolution, while the Neandertal Phase model concludes that Neandertals were vital in the formation of later European populations. This theme of Neandertals ultimately not contributing to the formation of the populations that follow them can be seen in the development of all major models of Late Pleistocene European evolution that were created in the 20th and 21st centuries, such as Recent African Origin (RAO), Afro-European Sapiens/African Hybridization and Replacement (AES/AHR), Multiregional Evolution (MRE), and the Assimilation Model (AM).

It is generally accepted that Neandertals survived in Europe until approximately 30,000 years ago (Finlayson et al. 2008; Finlayson et al. 2006). EMHs arrived in Eastern Europe by no later than 40,500 years ago (Rougier et al. 2007; Trinkaus et al. 2003; Zilhão et al. 2007). This allows for a potential period of temporal and geographic

overlap of a minimum of 10,500 years. In order to examine hypotheses found in the paleoanthropological literature concerning Neandertal and EMH population dynamics, it is important to test whether Neandertals and EMHs temporally and geographically overlapped. Overlap between the two populations could then allow for hypothesized scenarios of admixture or competitive exclusion to occur. Conversely, if Neandertals and EMHs did not overlap, then the majority of the proposed methods of Neandertal extinction could not have taken place.

Proposed models of Neandertal extinction and EMH expansion offer hypothesized patterns of geographic and temporal placement of these two populations that can be tested with Ecological Niche Modelling (ENM) methods. ENM focuses exclusively on examining the geographic correlation between a sample of known locations and environmental variables. Only climatic and topographic environmental variables are considered, such as elevation and precipitation. ENM methods offer a novel approach to investigating questions of Late Pleistocene hominin population dynamics by allowing researchers to model the geographic extent of a group's fundamental niche parameters, or, where a sample's fundamental niche parameters would allow them to survive. This would result in their predicted presence and absence in geographic space.

One model which has been proposed to explain the pattern and mode of Neandertal extinction and EMH expansion on the Iberian Peninsula is the much discussed Ebro Frontier Model (EFM). Based primarily on archaeological evidence, the EFM hypothesizes that EMHs were prevented from accessing the southern part of the

Iberian Peninsula until approximately 35 ky cal BP. This geographic discontinuity between hominin populations is proposed to have been caused by ecological differences between the northern and southern areas of the Iberian Peninsula (Zilhao 1997; Zilhão 2000; Zilhão 2009). This hypothetical model asks questions which can be tested with ENM methods such as the ones used in this dissertation. However, rather than confining itself to analyzing only the Iberian Peninsula, this dissertation takes a continent-wide approach. Expanding the samples past the borders of the Iberian Peninsula drastically increases the sample sizes and thus allows the project to have a better chance of building stronger predictive models.

This dissertation uses the Genetic Algorithm for Rule-Set Prediction (GARP) to examine the correlation between presence points representing late surviving Neandertals and EMHs with three paleoenvironmental reconstructions for the time period immediately preceding Neandertal extinction, spanning the period from 43.3 to 36.5 ky cal BP. GARP produces presence/absence maps of the geographic extent of the suitable habitat, or fundamental niche parameters, for the sample in question based on the specific nature of the environmental variables found at those sites. The three paleoenvironmental reconstructions used in this dissertation cover the period of 1) Pre-Heinrich Event 4 (Pre-H4) from 43.3 to 40.2 ky cal BP, 2) Heinrich Event 4 (H4) from 40.2 to 38.6 ky cal BP, and 3) Post-Heinrich Event 4 (Post-H4) from 38.6 to 36.5 ky cal BP (Banks et al. 2008b). Location data here were organized into several different samples: A) sites that have produced morphologically diagnostic Neandertal remains, B) sites that have produced Middle Paleolithic (MP) artifacts, but no Neandertal remains,

C) a combination of the previous two samples, and D) sites that have produced Upper Paleolithic (UP) artifacts. A separate sample of morphologically diagnostic EMH remains dating to this time period in Europe was not included in the study as the number of pertinent sites fell below the requirements of necessary sample size needed to produce reliable results with GARP. Due to this constraint, locations of Upper Paleolithic sites must be used as a proxy for EMH presence.

The three major questions of this dissertation research are listed below.

1) What are the patterns of predicted presence and absence of Neandertals and EMHs in Europe prior to Neandertal extinction and how do those patterns fluctuate?
2) How similar or distinct are the patterns of the fundamental niche parameters for these populations?
3) What is the nature of the geographic and temporal overlap of Late Neandertal and EMH fundamental niche parameters and predicted presence in Europe during the time period of 43.3 – 36.5 ky cal BP?

The answers to the above questions will not only tell us about the extent of Neandertal and EMH suitable habitat, but will also offer insight into the population dynamics of the two groups and the behavioral responses of each group to fluctuating climate. In addition to examining the two primary questions described above, this dissertation also investigates secondary topics that center on common assumptions made in anthropological literature, the nature of the available samples, and the ability of those samples to answer the above questions. These topics include:

A. Are samples of Neandertal fossil locations, MP, and UP sites able to create predictive models that can predict test points at a better than random rate? In other words, can each of these samples create statistically valid models when tasked with predicting locations of the same type?
B. Do samples exclusively made up of MP archaeological sites have the ability to correctly predict locations of Neandertal fossil sites from the same time period at a better than random rate? Or, what is the nature of the interpredictivity of archaeological and fossil remains?

Question B of the secondary goals directly addresses the common assumption in anthropology that stone tool technocomplexes can be used to infer biological presence and population dynamics. Recent research has demonstrated that this assumption is not always valid (Maroto et al. 2012). This secondary goal is to quantify the relationship between MP tools and Late Neandertals and to examine if the statistical power of that interpredictivity fluctuates over time.

This dissertation is divided into seven sections. Section 2 discusses the previously mentioned evolutionary models of Late Pleistocene hominin evolution in Europe. This section details the historical context and development of the models and their predictions for hominin behavior in Late Pleistocene Europe. Section 3 addresses previous anthropological research using ENM methods and the theoretical constraints of ENM research as shown by previous work in other fields. Section 4 covers the materials used in this study, including the location samples of Neandertal fossil remains, MP, and UP sites, along with the paleoenvironmental reconstructions used by the GARP program

to generate the predictive models. Section 5 details the methodology used for each experiment conducted in the course of this dissertation research, including experimental design, map generation, and statistical validation. The results of each experiment are discussed in Section 6 with the discussion and conclusions of this research following in Sections 7 and 8. Additional maps and data are included in the appendices.

2. MODELS OF LATE PLEISTOCENE EVOLUTION

This project's theoretical framework is rooted in the development of theories concerning the possible presence of interaction between Neandertals and early modern human (EMH) populations as well as the nature of that interaction, if it did occur. The major theme in this research is to integrate modern anthropological theory with the interpretation of topographic and paleoenvironmental studies. This section discusses the creation of the competing models of Late Pleistocene hominin evolution in their historical context with an emphasis on what these models predict for Neandertal and EMH behavior, rather than their evolutionary relationship specifically. The question this dissertation asks is not centered on Late Pleistocene populational taxonomic relationships, but rather on what the nature of these two populations' geographic distribution could have been and how that might have affected their interactions with one another. In this manner, this dissertation takes a different approach than what has been traditional in paleoanthropological theory building, where the majority of previous work has focused on determining the nature of Neandertal vs. EMH taxonomic affinity and, thus, whether or not these two populations could have successfully experienced admixture.

Ultimately, the nature of the arguments concerning Neandertal taxonomy can be boiled down to the question of whether or not Neandertals and other archaic hominin populations contributed to later fully anatomically modern populations. While this dissertation does not seek to answer this question, it is vital to understand the importance

that has been placed on this topic. In anthropological theory, this has been the most common way to frame the debates surrounding Middle and Late Pleistocene hominin evolution until very recently. However, while Late Pleistocene hominin evolutionary theory has historically been framed in this manner, the body of evolutionary theory can also be interpreted in how it pertains to Neandertal and EMH behavior.

2.1 Historical Context

Since the 1856 discovery of the first Neandertal specimen at Kleine Feldhofer Grotte, in the Neander Valley of Germany, anthropologists have been interested in answering the question of Neandertal taxonomic identity and whether or not Neandertals and modern humans were separated at the species or subspecific level (Trinkaus 1986). This question is part of the debate surrounding the possible contribution of Neandertal genetic material to contemporary EMH populations and the forces driving Neandertal extinction versus EMH expansion. Historically, there has been a large amount of focus in European Late Pleistocene models of hominin evolution on determining whether or not Neandertals had the ability to admix with EMH populations. This emphasis has tended to take the form of determining how recent hominin evolution led to modern humans, rather than examining Late Pleistocene evolution and population dynamics in Europe as they stand alone (Trinkaus 2005). In Europe specifically, the emphasis of these models has historically centered on Neandertals and whether or not they could have contributed to or evolved into modern European populations (Trinkaus and Shipman 1993). This overwhelming emphasis on taxonomy is, as Trinkaus states, "…

not a question addressing the evolutionary processes involved in the emergence of modern human biology. This is a question regarding the evolutionary purity of living humanity" (2005:218).

The discussion also tends to be largely Euro-centric, focusing on whether or not Neandertals could have contributed to modern European populations (Trinkaus 2005). This is partially due to a greater body of research having been conducted in Europe than in other continents, resulting in the assumption that we know more about this area since it has been studied more extensively (Aiello 1993). In some cases, the theories that were developed to explain the perception of the European fossil hominin record were directly applied to other geographic areas and times (Smith et al. 1989; Trinkaus and Shipman 1993). This occurred without the realization that answers to evolutionary questions in Europe might not explain questions regarding human evolution in other areas of the Old World. Paleoanthropology has, fortunately, come to the realization that hominin evolution was an incredibly complex process and the forces acting in one area at one time may not be the same in other areas and at other times (Relethford 2008; Trinkaus 2005; Wolpoff et al. 2000).

2.2 Early Twentieth Century

The models of Late Pleistocene hominin evolution currently debated in the literature have their roots in models created during the first half of the 20th century. Three main models regarding Neandertals and their relationship to modern humans were identified by Vallois (Smith et al. 1989; Vallois 1958). These hypotheses, though now

defunct, are important in the history of the debate concerning the fate of the Neandertals and the origins of modern humans. This history has helped to frame the debate on Late Pleistocene European hominin evolution. Two main competing models were developed in the 1920s: the Presapiens model and the Neandertal Phase model. They mirror the current day discussion in that one camp states that Neandertals were replaced by modern humans and did not contribute to later hominin populations, while the other hypothesizes that Neandertals had a much larger part to play in the origins of modern humans. The same themes and questions have been the topic of intense paleoanthropological debate for the last 90 years.

2.2.1 The Presapiens Model

The Presapiens model, created by Boule in the 1920s (Smith et al. 1989) and further developed by Vallois in the early 1950s (Vallois 1954), contends that modern humans evolved in-place in Europe, but were not descendants of Neandertals (Smith et al. 1989). Marcellin Boule, one of the scientists who spearheaded much of the early development of 20th century Neandertal studies, was one of many who held the view that Neandertals were essentially too deficient to have contributed to the modern human lineage. Boule stated that, "*Homo Neandertalensis* is an archaic species of man. It was abruptly followed by the Aurignacians, who differed from the Mousterians as much in their superior culture as in the superiority or diversity of their physical characters" (Boule 1923). Neandertals were commonly described in the academic literature of the time as retrograde, coarse, backward, and extremely inferior to modern humans in every

possible way (Boule 1921; Boule 1923; Burkitt 1921; MacCurdy 1924). The behavioral implications of the Presapiens model are quite clear. Neandertals were a failed offshoot of the hominin lineage that never contributed to later modern populations. Under this model, if Neandertals interacted with modern humans at all, they did not experience admixture and were quickly replaced by modern humans, then considered to be the qualitatively superior species.

Much of the idea that Neandertals were somehow deficient originated in Boule's work reconstructing and describing the La Chapelle-aux-Saints specimen. According to his interpretation, Neandertals were brutish and unintelligent, could not have walked fully erect, and had opposable toes (Boule 1921). His analysis was the most comprehensive one on a Neandertal at the time of its publication. Much of his conclusion that Neandertals could not have contributed to later modern human populations was based on the apparent traits that, to Boule, indicated the La Chapelle specimen was not fully bipedal. However extensive Boule's research on La Chapelle was, he apparently was not aware of or ignored publications that addressed the polytypic nature of human morphology for populations that existed outside of Europe. It also appears that he may have placed less emphasis on morphological characters that did point to fully erect posture for La Chapelle. Boule also did not discuss the evidence of extensive osteoarthritic changes on the individual (Hammond 1982).

Scientists have since reanalyzed his reconstruction and found the majority of Boule's conclusions to be in error. Despite this, his interpretation dominated paleoanthropological thought for many years (Drell 2000; Hammond 1982; Trinkaus and

Shipman 1993). This image was introduced to the non-academic public in the form of an illustration by Frantisek Kupka published in 1909 in both *L'Illustration* and *The Illustrated London News* (Figure 1). This illustration was based on Boule's interpretation of the La Chapelle-aux-Saints specimen, which was the most complete Neandertal skeleton known at the time (Hammond 1982).

Figure 1. Illustration based on Boule's work by Kupka (1909).

In 1908 when Boule published his analysis of the La Chapelle specimen paleontology, the validity of evolution had only recently been accepted by academic circles. Since the discovery of the Feldhofer specimen from the Neander Valley,

Germany, the debate had only just begun to move past the thought that these individuals were diseased or pathological modern humans. His arguments on Neandertal taxonomy and morphology were so well accepted that it was 40 years until the La Chapelle skeletal material was re-examined in the mid-1950s by WL Straus and AJE Cave. Straus and Cave pointed out that the postural abnormalities noted by Boule were caused by extensive osteoarthritis. Boule did mention that osteoarthritis was present on La Chapelle, but only in passing. Had Boule acknowledged the importance of other data available at the time, his specific conclusions concerning this Neandertal specimen could have been quite different than what was published. There has been a large amount of debate on Boule, his conclusions, and his possible motivations in Neandertal research (Hammond 1982).

At the time Boule published his reconstruction of La Chapelle, the questions of whether or not evolution applied to humans and what to do with the Neandertals dominated academic discussion. Boule had the opportunity to add greatly to the debate of whether or not Neandertals contributed to contemporary European modern human populations. He felt that he had solved the dilemma with his analysis, as did many others. While his specific conclusions on the morphological and behavioral characteristics of Neandertals have been refuted, Boule did contribute some portions of the theoretical framework of paleoanthropological study that still hold true today. With his extensive study of the La Chapelle specimen, he demonstrated to the scientific community that the same principles of evolutionary theory that applied to the rest of the biotic world also applied to the human lineage. And, despite the fact that nearly all of

Boule's anatomical conclusions have been since found to be in error, he did establish human paleontology as a valid science (Hammond 1982; Trinkaus and Shipman 1993).

Boule was not the only paleontologist essential in the formation of the Presapiens hypothesis. Sir Arthur Keith, who had formerly believed Neandertals were the ancestors of modern Europeans, became one of the fiercest supporters of the Presapiens model. The sample of fossils used by supporters of the Presapiens model are a curious mix of specimens, some of which have now been shown to be younger than previously assumed or even outright hoaxes. A few specimens belonging to the former category included Galley Hill and Ipswich. The most notable specimen belonging to the latter category is, of course, Piltdown Man, known at the time as *Eoanthropus dawsonii*. The Moulin Quignon mandible was also used as evidence in support of the Presapiens model and, while it does not appear to have been faked in the same manner as Piltdown, it does appear to be a modern mandible that was used to seed a site (Trinkaus and Shipman 1993).

As Trinkaus and Shipman describe the Presapiens model:

> "As formulated by Keith and Boule, the pre-Sapiens theory argued that large-brained, modern-skulled humans were so distinctive that they must have had a long (and honorable) evolutionary history…Boule and Keith were distinctly uncomfortable with any suggestion that we might have been descended, relatively recently, from anything less human than ourselves. They preferred to believe that pre-Sapiens humans existed far back into the

Pliocene…relegating all known fossil hominids to aberrant side-braches on the family tree" (Trinkaus and Shipman 1993:308).

The tenets of the Presapiens model require certain behaviors of both Neandertals and modern humans. The lineages leading to Neandertals and modern humans were concluded to be deep and ancient. These two apparent lineages never admixed and remained completely separate throughout space and time, though both populations are theorized to have originated in Europe. The Presapiens model is not clear on whether the hypothesized lineage that ultimately led to modern humans existed in Europe side-by-side with the purported Neandertal lineage, or if that population left Europe early and evolved into modern humans outside of Europe (Hrdlička 1927).

While the Presapiens models was largely accepted in the scientific community in the first half of the 20th century, there were some dissenting voices. Aleš Hrdlička, in a critique of the Presapiens hypothesis, summarized the model as the following:

> "It has been decided, on the weight of a limited initial group of specimens, that Neandertal man was a man of a different species; that he may possibly have originated from his European predecessors, but that, after a long period of existence and after having spread far and wide, he perished abruptly and completely, without leaving any progeny, on the approach of a superior species, the *Homo sapiens*" (Hrdlička 1927:270).

The Presapiens model and its implications for Late Pleistocene hominin evolution remained the one accepted by most of the scientific community for over forty years. However, with the discovery that Piltdown was a hoax, paleoanthropologists were

required to take a hard look at the fossil record, Late Pleistocene hominin evolution, and how Neandertals and EMH fit into the scheme of modern human origins. With additional fossils and the introduction of absolute dating, the picture of hominin evolution across the Old World became increasingly complex and, rather than ending the debate concerning Neandertals and modern human origins, new questions were ignited in the mid-twentieth century.

2.2.2 The Neandertal Phase Model

The Neandertal Phase model grew out of unilineal evolutionary models created by Schwalbe, Gorjanović-Kramberger, and Hrdlička. Hrdlička developed the Neandertal Phase model largely in response to what he saw as deficiencies in the Presapiens model and to the apparent levels of dogma he saw in the field for arbitrarily accepting that model without question. The hominin fossil record in the 1920s was not as well-resolved as it is today and the largest number of Neandertal and EMH fossils were confined to Europe. Hrdlička took issue with what he saw as undeveloped ideas of where the alternate lineage leading to modern humans existed, as well as the assumptions that Neandertals were inferior to modern humans (Hrdlička 1927)(Hrdlička 1927).

This hypothesis states that Neandertals were directly and solely ancestral to modern humans (Smith et al. 1989). Hrdlička wrote his seminal paper "The Neandertal Phase of Man" in 1927 for the Huxley Memorial Lecture in response to the doctrine of the time that stated the Neandertals were simply a dead-end offshoot of the human genealogical tree that did not contribute anything meaningful to modern humans.

Hrdlička took a more measured view of the extent of the knowledge on Neandertal fossils that were available to paleoanthropologists in the 1920s.

> "The problem of Neandertal man, as it now exists, presents the following uncertainties:—It is not yet properly known where, when, and how he began, and how far eventually he extended geographically; it is not yet definitely known just who he was and what were his phylogenetic relations to the man that succeeded him; and it is not known plainly just why and how he ended, and whether or not he left any progeny. Besides which there are still but more or less vague notions regarding the exact length of his period, his average physique, his variations and sub-races, the reasons for his relatively large brain, his changes in evolutionary direction. And there are other uncertainties. It thus appears that, notwithstanding his already numerous collected remains, Neandertal man is still far from being satisfactorily known to us taxonomically, chronologically, and anthropologically" (Hrdlička 1927:250).

Hrdlička was one of the first to propose that Neandertals were not as stupid or backwards as was predominantly believed by the Presapiens camp. Through analysis of the archaeological record known at the time between Acheulean, Mousterian, and Aurignacian sites, he proposed instead that Neandertal behavior appeared to be similar to the populations that both preceded and followed them (Figure 2). He is also one of the first to argue that Mousterian tools were not somehow inferior to the technocomplexes assumed to be the product of modern humans.

The fossils considered by Hrdlička (1927) to represent the Neandertals are as follows: Gibraltar I, Neandertal, La Naulette, Šipka, Spy I and II, Bañolas, Malarnaud, Krapina, Le Moustier, La Chapelle, Jersey, La Quina, La Ferrassie, Ehringsdorf-Weimar, Galilee, Erhingsdorf-Fischer's Quarry, and Gibraltar (child). This sample includes Proto-, Classic, and late Neandertal specimens. The specimen simply listed as Galilee is the specimen recovered from Mugharet el-Zuttiyeh, discovered in 1925 by F. Turville-Petre (Hrdlička 1927). Within the next 4 years, the sites of Amud and Tabun would also be introduced to paleoanthropologists. While none of the specimens classified as Neandertals in this sample have been reclassified to another taxonomic group, their dating has been revised over the years.

Food, and Habits Relating Thereto.

Acheulean Man.	Mousterian Man.	Aurignacian Man.
Chiefly a hunter. Fisher (?). Use of molluscs—no trace. Knew fire. Preparation of food: probably by roasting on fire or coals—no trace of any vessels for boiling.	Chiefly a hunter. Fisher (?). Use of molluscs—no trace (?). Knew fire. Preparation of food: probably by roasting on fire or coals—no trace of any vessels for boiling.	Chiefly a hunter. Fisher (probably). Use of molluscs (?). Knew fire. Preparation of food: probably by roasting on fire or coals—no trace of any vessels for boiling.

Food, and Habits Relating Thereto—continued.

Acheulean Man.	Mousterian Man.	Aurignacian Man.
No agriculture. No domestication of animals. Bones broken for brains and marrow. Bones and refuse accumulations in inhabited caves, and in front of them. No trace of storage of food. Pictorial representation of hunted animals—not known.	No agriculture. No domestication of animals. Bones broken for brains and marrow. Bones and refuse accumulations in inhabited caves and in front of them. No trace of storage of food. Pictorial representation of hunted animals — none known yet.	No agriculture. No domestication of animals. Bones broken for brains and marrow. Bones and refuse accumulations in inhabited caves and in front of them. No trace of storage of food. Pictorial representation of hunted animals — gradual development.

Figure 2. Hrdlička's (1927:257-258) description of his hominin phases.

The Neandertal fossils discussed above were contrasted with the osteological remains that were considered to be representative of the modern humans that immediately followed the Neandertals during the Aurignacian. These include: Most/Brüx, Combe-Capelle, La Rochette, Camargo, Castillo, Hohlefels, Enzheim, Mentone, Paviland, and Ojeów. Specimens from Brno, Předmosti, and Solutré are listed by Hrdlička as "Aurignacian, probably" and Cro-Magnon and Halling are designated as "Aurignacian or later" (Hrdlička 1927).

The EMH fossil record has changed significantly since the 1920s. Even shortly after the Most/Brüx skull was discovered in the early 1900s, paleoanthropologists were unsure of its ancient status and it has since disappeared from academic analysis (Smithsonian Annual Report 1907). Combe-Capelle, long considered an example of EMH in western Europe, has since been redated to ~7 ka (Valladas et al. 2003). The remains from the Spanish site of Camargo, discovered in 1908, were destroyed during the Spanish Civil War before a formal analysis could be published (Churchill and Smith 2000).

The specimen Hrdlička refers to as "Castillo" is one of the specimens from the human remains discovered by Obermaier prior to World War I at the site of El Castillo, Spain: a partial mandible from a juvenile, probably between the ages of 3-5, unnamed cranial fragments, and a lower right second molar. However, these specimens disappeared prior to their publication and the association of these specimens with UP technologies is not concrete (Hublin 2013). A previously unpolished manuscript by Vallois was released to the public by Garralda (1992), but both the morphological and

archaeological association of these lost specimens is currently considered unclear (Hublin 2013).

The specimen listed as Enzheim was included in several publications as representative of modern humans dated to the Aurignacian during the 1920s and 1930s (Hrdlička 1927; Lipman 1934; Morant 1930; Tilney 1927), but it has curiously faded from study. It is not clear whether or not the remains were lost or simply reclassified as belonging to a later date. The specimens listed as Mentone refer to the burials at Grotta del Caviglione, Grotta dei Fanciulli (also known as Grotte des Enfants), and Grotta del Principe in Italy. The name Mentone is no longer used to refer to this location in academic literature (Pettitt 2011). It is not clear to which specimen Ojeów refers. It, like Enzheim, has disappeared from current paleoanthropological analyses. The specimen Hrdlička names as Halling is also known popularly as "Halling Man" and has since been reclassified as Neolithic in age.

At the time that Hrdlička developed the Neandertal Phase model, he saw little evidence for an alternate lineage leading to modern humans existing outside of Europe, nor one that existed in Europe contemporaneous with Neandertals. Instead, he proposed that the more parsimonious explanation was that Neandertals evolved into Aurignacian humans and then into modern humans (Figure 3). He proposed that this evolutionary process was spurred rapidly by environmental changes (Hrdlička 1927).

It is important to note that many of the arguments made by both the Presapiens and Neandertal Phase camps are eerily close to those made by supporters of Replacement and Multiregional Evolution (MRE). Boule's and Hrdlička's models were

the original sources of Replacement and MRE and their views still influence our interpretation of the investigation of modern human origins and Neandertal extinction to this day.

> "The sponsors of the view that Aurignacian man was a man of different and superior species to the man of the Mousterian period, conceive him for the most part, apparently, as an invader who came from somewhere outside the Neandertal area, overwhelmed completely the established less capable species, and annihilated or at least wholly replaced it, over all the great domain over which it once extended" (Hrdlička 1927:259).

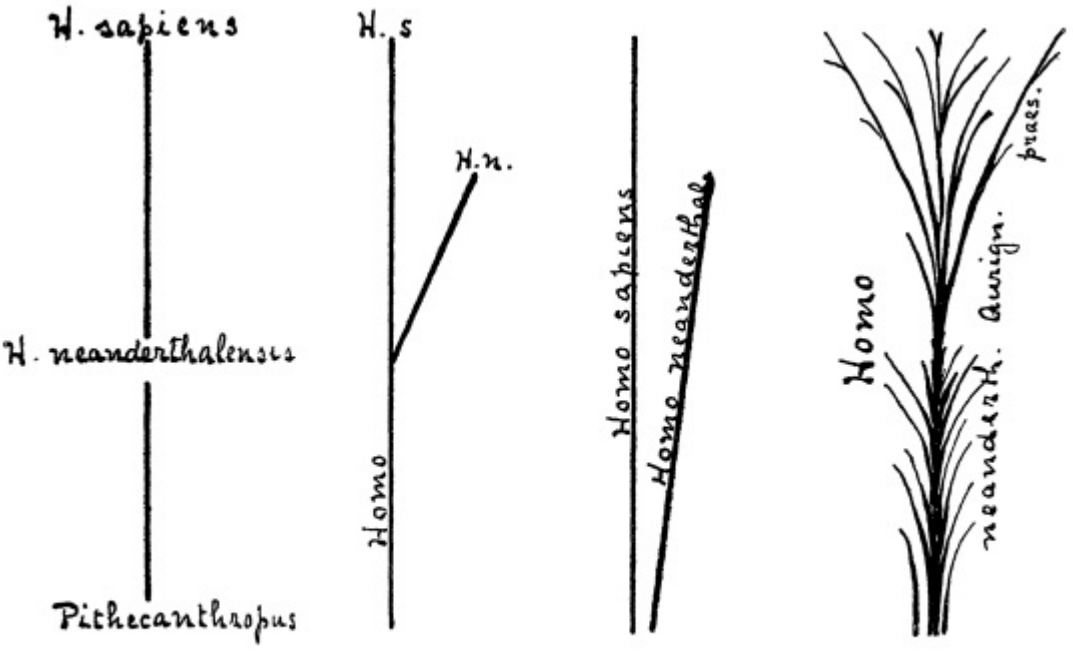

FIG. 5.—VARIOUS CONCEPTIONS AS TO THE PHYLOGENETIC RELATION OF NEANDERTHAL AND LATER MAN.

(Present evidence favours the view represented on the extreme right.)

Figure 3. Hrdlička's (1927:272) illustration of the then current evolutionary models of Late Pleistocene evolution.

While Hrdlička and a few other scientists created the Neandertal Phase model, they were by far the minority opinion. Le Gros Clark stated that the hominin specimens from the Mount Carmel area, believing them to be ancient and Neandertal, were indicative of an evolutionary phase between *Homo sapiens* from the pre-Mousterian and later Neandertals (Clark 1955; Howell 1957). The vast majority of the scientific community during the first half of the 20th century viewed Neandertals as dead end side-branches of the lineage leading to modern humans. Neandertals and EMH were nearly always studied as they related to the appearance of modern humans and, typically, how archaic hominins could have led to modern Europeans, specifically. This is a problem that still plagues paleoanthropology today (Relethford 2008; Relethford 2001; Trinkaus 2005; Trinkaus and Shipman 1993). Paleoanthropologists' interpretation of the fossil hominin record and the prevalent models of Late Pleistocene hominin evolution had to undergo a major revision with the addition of many new fossils and the exposure of "Eoanthropus dawsonii" (i.e. Piltdown Man) as a hoax.

2.3 Mid-Twentieth Century

The mid-twentieth century brought about many changes for studies concerning hominin evolution. New data in the form of new fossils and the advent of absolute dating methods greatly revised the landscape of the dataset paleoanthropologists used to generate theories on Late Pleistocene hominin evolution. This greatly reformed fossil record required anthropologists during the mid-part of the 20th century (from the 1940s through the 1960s) to revise models of hominin evolution. However, even with all of the

new data, anthropologists settled themselves into two basic competing camps in regards to Late Pleistocene evolution in Europe: those that thought Neandertals mattered and those that did not. Those researchers that supported the idea that archaic populations had a part to play in Late Pleistocene hominin evolution (both in Europe and throughout the rest of the Old World) formed the basis of what would become known as Multiregional Evolution (MRE). The contentious nature of the discussion between the two camps remained and academic discussion was fraught with misunderstandings of the basic tenets of both bodies of theory.

Models such as the Neandertal Phase, Presapiens, and Pre-Neandertal models, helped shape the framework in which later models of modern human origins were created, such as the Multiregional Evolution (MRE), Assimilation (AM), and Recent African Origins (RAO) models. It should be noted that all three of these early models discussed in Section 2.2 (the Neandertal Phase, Presapiens, and Pre-Neandertal models) refered only to European prehistory. Those models assume that modern humans originated, or evolved, in Europe rather than any other part of the Old World. Such is the case even with the Pre-Neandertal model, where modern humans were hypothesized to have evolved outside of Europe, but only after their ancestral population is hypothesized to have originated in Europe (Howell 1951; Howell 1957; Smith et al. 1989). These models were created prior to the realization of the incredible importance that the African continent played in human evolution and are, thus, extremely Eurocentric. The Eurocentrism in these models is partially due to the fact that the majority of the paleoanthropological research at the time had been conducted in Europe. The fossil

record in the remainder of the Old World was not as well known by European scientists (i.e. those scientists that were creating evolutionary theory) (Smith et al. 1989; Trinkaus and Shipman 1993).

2.3.1 Death of the Presapiens Model

The discovery of the Piltdown forgery caused a conundrum for supporters of the Presapiens model. Piltdown had historically been considered the most solid piece of evidence supporting the hypothesis that Neandertals went extinct without contributing to modern populations and that modern humans evolved in place in Western Europe. While there were always scientists who doubted the validity of the Piltdown specimen, or at least doubted its significance in some form, it is important to note how well Piltdown was received by a large portion of the academic community and that it was not discovered as a hoax until Weiner, Oakley, and Le Gros Clark's 1953 publication (Oakley and Weiner 1955; Weiner and Oakley 1954; Weiner et al. 1953).

Piltdown was accepted as valid and ancient because it appeared to confirm the majority of the Presapiens hypotheses about how modern humans evolved: 1) with its large braincase it supported the hypothesis that brains grew larger before faces became more gracile (Oakley and Weiner 1955) and 2) its discovery in Europe (and specifically England) supported the belief that modern humans were ultimately European in origin. This second point reinforced the idea that all other fossil hominins that had been discovered up to that point were extinct side branches of human history which disappeared without issue and without contribution to later modern human populations.

It also reinforced insidious notions that Europeans were the primary population of modern humans and thus every other modern population throughout the world was somehow a degenerated form of European. This allowed Europeans to reinforce the notion that they were somehow superior to all other populations on earth. This idea is, of course, wrong and terribly misinformed, but it persisted within the scientific community for many years. Piltdown might have been exposed as a hoax much earlier if this racist dogma had not had such an unfortunate hold on the scientific community.

Even with the highly revised fossil record from the 1900s to the mid-twentieth century, it is impossible to deny the fact that later replacementist or migration-based models have their origins in the previous Presapiens model. They thus inherit much of the theory that was created by scientists like Marcellin Boule and Arthur Keith, whereby Neandertals are relegated to a dead end side branch of hominin evolution and were replaced by modern humans in Europe. One of the most prominent anthropologists to attempt to revise the Presapiens hypothesis during the mid-20th century was Henri Vallois, a former student of Marcellin Boule. He readily acknowledged the blow that the Piltdown hoax dealt to the Presapiens model and chose to emphasize other fossil hominins as evidence in support of it (Smith et al. 1989; Trinkaus and Shipman 1993; Vallois 1958).

Vallois still felt that, in spite of the revision of the fossil record and the exclusion of Piltdown, modern humans' large cranial capacities were distinct enough to warrant an extremely long evolutionary timescale. This evolutionary history was typically hypothesized by Presapiens supporters to extend back into the Pliocene (Trinkaus and

Shipman 1993). In addition to the removal of Piltdown from the fossil record, specimens from Galley Hill, Moulin Quignon, and Ipswich had also been eliminated from the pertinent sample. Vallois put much of his hopes for the Presapiens hypothesis in the specimens from Fontéchevade, which was then considered to be dated to the last interglacial based on their faunal association. However, this specimen was missing the supraorbital torus region. Of the reconstructions available, Vallois put stock in one that created a smooth and vertical forehead which he took to indicate that modern morphology was very old. Unfortunately for Vallois, it is much more likely that an accurate reconstruction of Fontéchevade 2 includes a much more robust supraorbital tori region (Trinkaus and Shipman 1993). In addition, recent work with radiocarbon and ESR absolute dating techniques has revised the age of Fontéchevade to OIS 3, or ~39 ky cal BP (Chase et al. 2007). This date would make the specimen representative of EMHs in France and not an earlier population as was previously proposed.

Vallois also continued to use the fragmentary cranial specimen found at Swanscombe, Kent, England, in support of the Presapiens model (Vallois 1958) based mainly on metric measurements from the partial reconstruction and the reconstructed cranial capacity of ~1,325 ccs, which is well within the range of modern humans (Morant 1930). This is also one of the only specimens used in support of the Presapiens model that has not been redated to a significantly younger time frame or been eliminated from the sample due to fraudulent practices. The most recent work in dating the fossil places it at no younger than ~390 ky cal BP (Stringer and Hublin 1999)(Stringer & Hublin 1999) and in OIS 11 (Bischoff et al. 2003). The most recent analyses of its

morphology emphasize that the suite of morphological traits found on Swanscombe show that there are archaic traits, and especially those indicative of later Neandertals. These traits include a convex occipital plane, a strong juxtamastoid ridge, and a suprainiac fossa (Hublin 1978; Hublin 2009; Hublin 1988; Santa Luca 1978; Stewart 1964; Stringer and Hublin 1999). The entire morphological suite taken in context of what we know currently about the Middle and Late Pleistocene hominin record, especially in Europe, indicates that the Swanscombe individual was ancestral to later European Neandertal populations rather than directly ancestral to the populations that would later result in the emergence of modern humans.

Vallois' work in the late 1950s was the last gasp for the traditional and strict interpretation of the Presapiens model. The majority of paleoanthropologists had taken into account the increased understanding of the fossil record and began moving away from the hypothesis of a deep temporal history on the European Continent for modern humans (Trinkaus and Shipman 1993). However, newer versions of replacement based models inherited much from the Presapiens models, including the need to relegate Neandertals to an extinct side-branch of hominin evolution that did not make any meaningful contributions to modern human origins.

2.3.2 Replacementism in the Mid-Twentieth Century

William W. Howells is often touted as one of the forefathers of modern replacementist models. His textbook, *Mankind in the Making*, first published in 1959, influenced an entire generation of emerging paleoanthropologists (Trinkaus and

Shipman 1993). Howells' interpretation of the fossil record known at the time of publishing *Mankind in the Making* is measured and thoughtful. He pointed out that theories of hominin evolution from Franz Weidenreich and Carleton Coon were more similar than many modern paleoanthropologists are comfortable admitting. In interpreting their work, WW Howells stated that Coon allowed for more admixture between populations of modern and ancient hominins than did Weidenreich (Howells 1967). However, a modern interpretation of both Weidenreich and Coon's research by Trinkaus & Shipman concluded the opposite (Trinkaus and Shipman 1993).

WW Howells' assessment of Late Pleistocene hominin evolution and the origins of modern humans is often painted as more extreme than is warranted by a close reading of *Mankind in the Making* (Howells 1967). At least in his seminal textbook, written later in his career, he takes a somewhat cautious approach when discussing the Middle and Late Pleistocene. He summarized:

> "…after about 35,000 B.C. we begin to see *Homo sapiens* widely spread in the Old World, and entering the New World as well…In the west the new men entered Europe; perhaps, in the early stages, the advance guard mingled with older types of man to produce what appear to be intermediate forms: mixing with the Neanderthals at Mount Carmel in Palestine, with the Rhodesians at Florisbad in South Africa, and with Solo Man in Southeast Asia or Indonesia. All this is less clear, and hypothetical in the extreme. But both Neanderthals and Rhodesians accepted their fate and vanished" (Howells 1967:346).

As indicated by the above quote, Howells acknowledged and accepted the possibility of admixture between modern humans and the archaic populations they may have encountered in different areas of the Old World. However, he does point out that much of that contact was not confirmed with the fossil evidence that they had access to in the mid-20th century. In short, at least later in his career, Howells was not as an extreme replacementist as he is often portrayed in the academic literature. Earlier in his publication history Howells does argue against including Neandertals as a direct ancestor to any population of modern humans. To clarify, he argued against Neandertals evolving directly into modern Europeans. He was somewhat more reticent in coming to a conclusion about whether or not Neandertals and modern humans could have interbred and produced fertile offspring (Howells 1942).

When examining the question of whether or not Neandertals were directly ancestral to all modern humans, WW Howells compared them to modern Australian Aborigines on the basis that native Australians also tended toward a suite of morphological robust cranial features. He argued that the suite of traits were different between the two groups and thus he argued against Neandertals as direct and sole ancestors for all modern human populations (Howells 1942).

> "The above is a purposefully emphatic statement of the argument that modern man as a whole is no descendant of the known Neanderthals, and he did not pass through a Neanderthaloid phase in his main line of ancestry. There remains the suggestion that one single race or another may be descended from the Neanderthal stock…The Skhul people are more of a borderline case and

> indeed have not been definitely assigned to *Homo sapiens*. But whatever be the explanation for this type, not even Keith and McCown find actual Neanderthal characters in it…Just what the Mount Carmel material proves can hardly be looked upon as settled. As for the rest, however, it does not appear that the distinction between Neanderthal man and anything known as sapiens has been obliterated, while on the positive side of the evidence is that the primitive sapiens ancestor was not of a Neanderthal character" (Howells 1942:189).

Prior to the development of the name "Out of Africa" to describe the hypothesis, it was also called "migrationism" or the Noah's Ark hypothesis in the 1970s (Howells 1976). As was seen in earlier versions of evolutionary models that exclude Neandertals from sole ancestry of modern humans, mid-20th century replacement or migration based models include a hypothesized single origin of the lineage that would eventually lead to the origin of *Homo sapiens*. The geographic location for the origin of this lineage was still debated. Louis Leakey was one of the first to propose that this area of origin was the African continent (Leakey et al. 1964; Leakey 1961; Trinkaus and Shipman 1993). It was hypothesized that modern populations, once they had radiated out from the place of origin, replaced archaic populations and did not experience admixture with them. It was also sometimes hypothesized that migrating modern populations did not encounter or overlap with archaic populations in Europe or Asia at all. Existence of temporal and geographic overlap between archaic and morphologically more modern populations was debated during this period, as it still is today in certain instances (Howells 1976).

By the 1970s, new lines of evidence began to be incorporated into the debate on the nature of Late Pleistocene hominin evolution. In addition to an ever increasing fossil record, genetic research made its first debut in paleoanthropological research. Most notable is the work by Cavalli-Sforza and Edwards on blood group frequencies and phylogenetics (Bertranpetit and Cavalli-Sforza 1991; Cavalli-Sforza 1966; Cavalli-Sforza and Edwards 1967; Cavalli-Sforza et al. 1988; Edwards and Cavalli-Sforza 1963; Edwards and Cavalli-Sforza 1964; Menozzi et al. 1978). The results of these studies were quickly incorporated into the arguments for single-origin replacement-based models and used to argue against multiregional models.

2.3.3 The Pre-Neandertal Model

F. Clark Howell postulated in publications from the 1950s that early Neandertals were ancestral to both Classic Neandertals and modern humans, but that modern humans evolved outside of Europe and thus were not direct descendants of Classic Neandertals. This hypothesis is called the Pre-Neandertal model (Smith et al. 1989). In other words, this model hypothesizes that the population ancestral to late Neandertals and modern humans was native to Europe, but then a group broke off and left Europe. The descendant population that left Europe then evolved into modern humans and later returned to Europe where they encountered their cousins the late Neandertals (Howell 1951). The Pre-Neandertal model appears to be the first attempt at creating an intermediary model of European Late Pleistocene hominin evolution taking into account the increased fossil record since the early 1900s.

F. Clark Howell (not to be confused with WW Howells) postulated in his 1951 paper "The place of Neanderthal man in human evolution," that early Neandertals were ancestral to both Classic Neandertals and modern humans (Figure 4). He includes Skhūl I, IV, V, VI, and IX in his early Neandertal group (Howell 1951). With the reorganization of the Levantine fossil record due to better absolute dating methods and a better understanding of Late Pleistocene hominin morphology, specimens recovered from Skhūl are now classified as EMH and not Neandertal. This would greatly influence and change the conclusions of Howell's 1951 paper. The inclusion of the specimens from Skhūl in Neandertals does indicate that, at least historically, robusticity was largely associated with archaic populations. Thus, it is not entirely surprising that the Skhūl individuals, displaying a larger range of robusticity that paleoanthropologists now know is common in EMH populations, were shunted into the Neandertal taxonomic box.

Based on the inclusion of fossils that we now know are not early and are not Neandertals, Howell concluded that, "The early Neanderthals are similar to modern man, and differ from the classic Neanderthals…Conversely, the classic Neanderthals differ from both the early Neanderthals and modern man" (Howell 1951). Based on the assumption that the specimens from Skhūl represented early Neandertals, Howell concluded that, since this early Neandertal group was more morphologically similar to modern humans, it was here that the evolutionary split between the Neandertal and modern human lineage occurred (Howell 1951; Howell 1957). Again, while F. Clark Howell's sample and conclusions have been disproven with increased knowledge of the

fossil record, we must remember that he was producing evolutionary theory with the fossil record that paleoanthropologists had access to at the time.

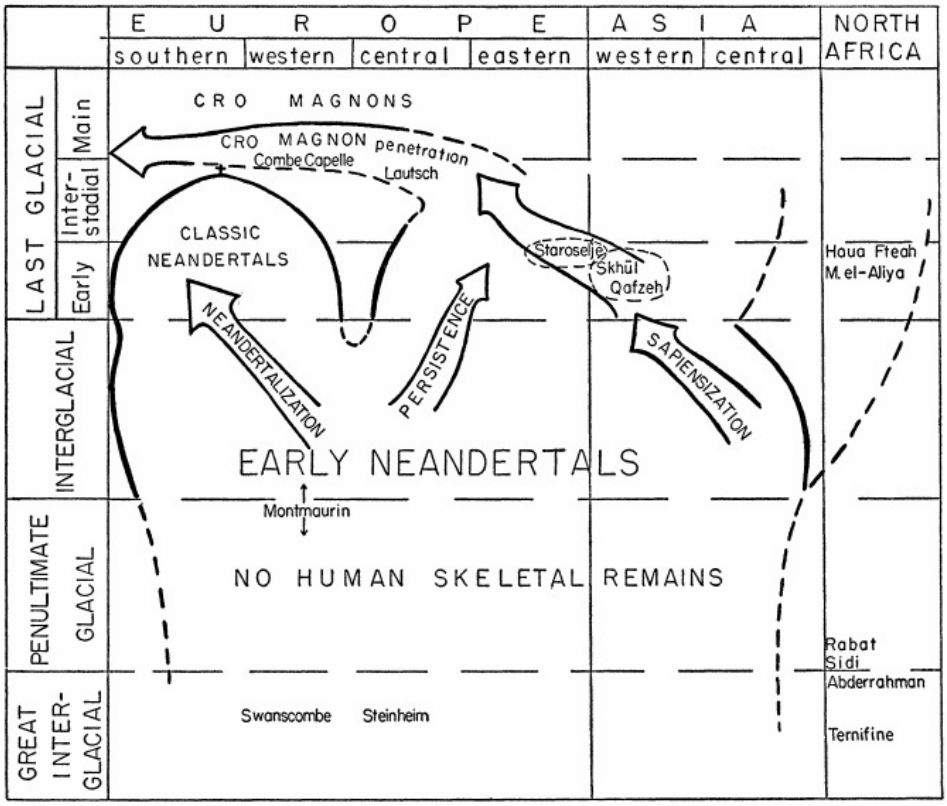

FIG. 4. TEMPORAL AND SPATIAL DISTRIBUTION OF "NEANDERTHAL" PEOPLES OF THE UPPER PLEISTOCENE AND OF THEIR MIDDLE PLEISTOCENE FORERUNNERS

Figure 4. Howell's proposed model of hominin phylogeny (1957:342).

Essentially, the Pre-Neandertal model argues that "early" Neandertals mattered in the grand scheme of modern human origins, but Classic and Late Neandertals did not. In response to the Presapiens hypothesis, Howell stated the following:

> "If such Neanderthal peoples, and their anatomically non-modern forerunners (Steinheim-Swanscombe, Montmaurin), were indigenous to the

> European area and 'pre-sapiens' peoples must have had an origin elsewhere and have subsequently expanded into (western) Europe. Where was this area and where is the fossil and other evidence necessary to support such an hypothesis?" (Howell 1957:342).

The Pre-Neandertal model of Late Pleistocene hominin evolution is an interesting one in that it removes Classic Neandertals from contributing to later modern European populations, but also gives importance to the hypothesized early Neandertals when discussing modern human origins. For hominin behavior, this model implies that one parent population existed in the Levantine area and then separated. The population in Western and Southern Europe evolved into Classic Neandertals while the population existing in Central and Eastern Europe, with influx from Western and Central Asia, evolved into modern humans. Despite their close geographic locations, these two populations remained separate until the Neandertals went extinct and modern humans remained. It should be noted that Howell's Pre-Neandertal model does not touch on the fossil record from Eastern Asia or sub-Saharan Africa that was known at the time and how it might play into Late Pleistocene hominin evolution.

2.3.4 The Birth of Multiregional Evolution (MRE)

The modern origins of Multiregional Evolutionary theory (MRE) began with Franz Weidenreich and his work examining hominin evolution. Though paleoanthropology had begun moving away from unilineal models of human evolution by the mid-20th century, MRE inherited some intellectual theory from the Neandertal

Phase model in the sense that MRE is seen to be in opposition to and in critique of fully replacementist models. In addition, MRE, like Hrdlička's Neandertal Phase model, separates itself theoretically from replacementist models by contending that archaic populations had some meaningful impact on or contribution to Late Pleistocene hominin evolution and the origin of modern humans, rather than relegating all archaic populations to extinct and unimportant side-branches.

Franz Weidenreich is usually credited with originating the first version of MRE in the late 1930s and through the 1940s. He began developing his theories on the process of hominin evolution in a way that was unique for the time period. Instead of focusing exclusively on the European fossil record, he started with evidence found only in Eastern and Southeastern Asia. He observed what he interpreted were indications of morphological continuity between the taxonomic group now known as *Homo erectus* (at the time they were variably known as "Pithecanthropus erectus" in Southeastern Asia and "Sinanthropus pekinensis" in Eastern Asia) and modern human populations in Asia (Aiello 1993; Weidenreich 1943a; Weidenreich 1945). For example, between *Homo erectus* specimens found in China and modern populations also located there, he observed that certain morphological traits were found in both populations. These traits include evidence of sagittal keeling, parasagittal depression, the presence of Inca bones, shovel-shaped lateral upper incisors, and others. In his analysis of "Sinanthropus pekinensis" he specifically stated that while he did observe morphological continuity and hypothesized an ancestral relationship between archaic and modern populations in China, "This statement, however, does not mean that modern Mongols derived

exclusively from *Sinanthropus* nor that *Sinanthropus* did not give origin to other races also" (Weidenreich 1943b:277).

Weidenreich introduced what is now called the trellis model (Figure 5) (Weidenreich 1947a) to synthesize his hypotheses of the nature of hominin evolution. When analyzing hominin evolution Weidenreich always stressed the importance of gene flow, "…the gradual evolving of modern man gives evidence that there must always have been an interchange between individuals or groups of individuals with differing morphological characters" (Weidenreich 1946). This is, perhaps, Weidenreich's greatest contribution to modern paleoanthropology. The realization that hominin evolution was made up of a series of interconnected populations became integral in the later versions of the MRE model and also many intermediary models.

Some parts of Weidenreich's hypotheses have since been disproven with the addition of new fossil material and dating methods, but his idea that gene flow was an important part of hominin evolution is difficult to deny with our current understanding of Late Pleistocene hominin evolution. In addition, Weidenreich was one of the first to recognize that there were many different ways to define a species and that choosing different definitions and applying them to the fossil record resulted in greatly varying interpretations (Weidenreich 1943a; Weidenreich 1946). In his syntheses of hominin evolution, Weidenreich emphasized the idea that archaic populations were evolving "toward" modernity more than paleoanthropologists do today. However, it was common until very recently in scientific circles to assume that there was some sort of higher goal actively directing human evolution rather than seeing evolutionary processes as reacting

to environmental stimuli. This view, now defunct, was a common failing in both the beginnings of MRE as well as replacement-based models. These mistakes were a product of the temporal context in which the models were created. The fact that these conclusions were a product of their time does not, perhaps, completely excuse the assumption that evolution has a goal. It should act as a cautionary tale that modern anthropologists not only inherit methodological tenets from previous research, but also that we are also not free from our own temporal influences. It remains to be seen how history will treat the theory that paleoanthropologists generate in the early 21st century.

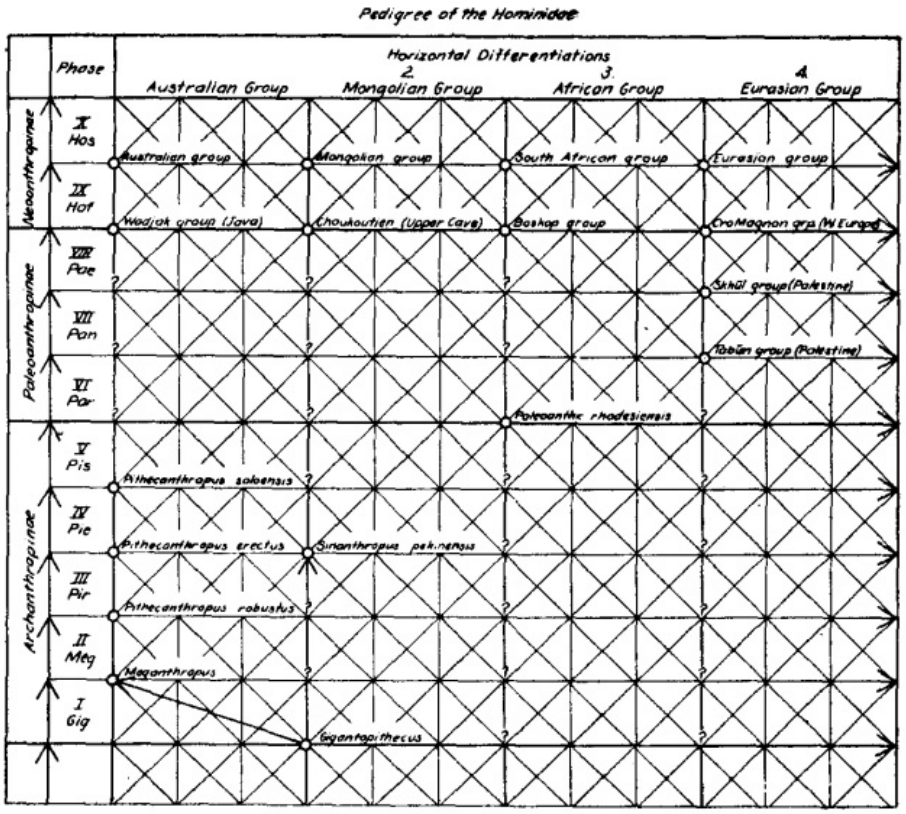

Figure 5. Weidenreich's (1947:201) original trellis model of hominin evolution.

When examining Weidenreich's hypotheses regarding Europe, Neandertals, EMH, and the origin of modern humans, he argues that Neandertals contributed to later modern human populations. Specifically, he argued that Neandertals should not be excluded from modern human ancestry due to their morphological traits, as had been argued by Marcellin Boule (1921), Arthur Keith (1915; 1925; 1931; 1948) and WW Howells (1967). Based on the known fossil record of the time, Weidenreich hypothesized that the root of the hominin lineage was in Asia rather than Europe, as had been commonly proposed by anthropologists. Regarding Neandertals and the origins of modern humans specifically, he stated,

> "The three phases of Paleoanthropinae are known from Africa, Asia and Europe: Rhodesian man (Par) represents the most primitive phase, the typical Neandertalians (Pan) represent the next phase, and the man of Weimar-Ehringsdorf, the man of Galilee or the Skhūl population of Mount Carmel the more advanced group (Pae)…The Skhūl group of Palestine presents forms intermediate between the typical Neandertal man from Tabūn and fossil modern man from Europe" (Weidenreich 1947a:200).

Here it should be pointed out that Weidenreich saw the Levantine Neandertals as ancestral to the Levantine EMHs from Skhūl and Qafzeh, which were directly ancestral to the European EMHs from sites like Cro-Magnon, France (Weidenreich 1947a). He was somewhat more cautious when examining the relationship between European Neandertals and European EMHs. Weidenreich hypothesized that they were connected in some way through gene flow, but perhaps were not directly ancestral to European

EMHs. However, he strongly objected to excluding the European Neandertals from the evolutionary history of modern humans simply on the basis of what he believed were minor differences. Specifically, while he agreed with his detractors that European Neandertals probably did not contribute to later SE Asian populations, he saw no reason for excluding Neandertals from even the possibility of having a meaningful impact on later modern human populations in Europe (Weidenreich 1941).

There are two main possible interpretations of a strict reading of Weidenreich's trellis model for Late Pleistocene hominin evolution and behavior in Europe. The first is one in which modern humans evolve in the Levant and then migrate into Europe where they came into contact with existing populations of European Neandertals. Under the tenets of this hypothesis, EMHs and the European Neandertals they encountered could have either experienced admixture or not. The only thing Weidenreich was quite clear about here is that there would be no reason to assume European Neandertals could not have experienced admixture with early modern humans (EMHs) (Weidenreich 1943a; Weidenreich 1947a). It is this interpretation of the trellis model with Weidenreich's emphasis on gene flow between hominin populations that largely influenced the later development and modification of MRE theory.

A second interpretation of Weidenreich's research, perhaps even more strict than the first, places more emphasis on what other anthropologists have called the polycentric nature (Howells 1967; Howells 1942) of the trellis model. Weidenreich does state that under his interpretation of the fossil record populations of archaic hominins would evolve into modern humans in different parts of the Old World. However, they would

not have evolved fully isolated from one another due to constant gene flow between different groups, as was implied by others' interpretation of his work (specifically WW Howells) (Weidenreich 1943a; Weidenreich 1943b; Weidenreich 1946; Weidenreich 1947a). A truly strict review of Weidenreich's original publications does need to acknowledge that he argued that modern human populations existing today in different regions of the Old World evolved from previous archaic populations in those regions in semi-independence from one another, though they never lost their ability to experience admixture with other populations. For example:

> "If we admit that mankind of today, uniform regarding its general character but differing special appearance, has developed from various regional stocks starting even from on *[an]* earlier stage than that represented by the Prehominids, and if we assume, furthermore, that development was not going on simultaneously everywhere but was accelerated in one place and retarded in another, perhaps as a consequence of local influences, then all the discrepancies between the morphologic and chronologic sequence of the known types of fossil man can be understood. The old theory, claiming that man evolved exclusively from *one* center whence he spread over the Old World each time afresh after having entered a new phase of evolution, no longer tallies with the paleontological facts. For *Pithecanthropus* and *Homo soloensis*, both inhabitants of the same region, represent undoubtedly subsequent stages of one and the same local Javanese branch of early man and prove thereby, at least so far as Java is concerned, that Java Man was tracing his own way in the direction of recent man

independent of what may have happened to similar stages in other parts of the world" (Weidenreich 1940:381-382).

The second interpretation of Weidenreich's work is no longer tenable with over 75 years of additional anthropological research. Some of his conclusions have been disproven given the state of our knowledge on hominin evolution and modern human variation today, including those that state there was a goal in hominin evolution of becoming modern, that human evolution stagnated in certain geographic regions, and that certain populations "achieved" modernity at different rates (Weidenreich 1940; Weidenreich 1947a). Weidenreich was a product of his time, one in which the majority of anthropologists held similar views. Other contributions he made have better stood the test of time, including those pointing out the importance of gene flow in hominin evolution. It is important to note that the later falsification of certain parts of Weidenreich's work does not discredit the entirety of his model of hominin evolution. The scientific process is designed to build upon disproven hypotheses and those revisions become building blocks for future work.

It is unfortunate that Weidenreich's theories of Late Pleistocene hominin evolution regarding the importance of gene flow were simplified in the academic literature by both his contemporaries and later anthropologists. WW Howells, whose work was some of the first to introduce multivariate statistics to paleoanthropology, portrayed Weidenreich's work as polygenic or polyphyletic in nature (Howells 1942). In other words, Howells simplified Weidenreich's hypotheses into the evolution of modern *Homo sapiens* in each geographic region of the Old World independent of each other

and experiencing little to no gene flow across those geographic boundaries. This form of evolution can be described as a candelabra model (Figure 6), rather than the trellis model proposed by Weidenreich (Figure 5).

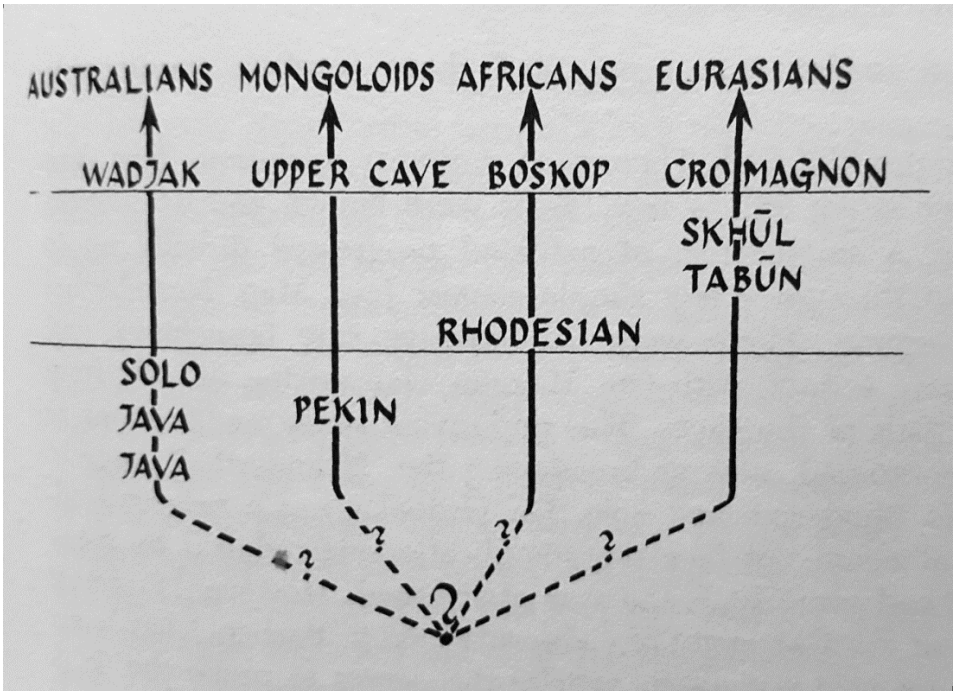

Figure 6. Howells' adaptation of Weidenreich's trellis model (Howells 1967:241).

It has been claimed by later paleoanthropologists that Howells' interpretation of this model of hominin evolution is so over-simplified as to be a misinterpretation of Weidenreich's theory (Trinkaus and Shipman 1993; Wolpoff et al. 2004; Wolpoff et al. 2000). This misrepresentation of MRE has plagued paleoanthropologists for decades. The misunderstanding was perhaps understandable at the beginning of the generation of MRE theory, but this incorrect interpretation has persisted long after the refinement of

MRE. WW Howells' interpretation of multiregional theory actually much more closely resemble the hypotheses put forth by Carleton S. Coon in his publications beginning in the late 1930s. Coon modified Weidenreich's original hypothesis and greatly deemphasized gene flow between geographic regions of the Old World, though he did not discount it entirely (Coon 1962). Specifically, in his book *The Origin of Races*, which he dedicated to Franz Weidenreich, he stated:

> "My thesis is, in essence, that at the beginning of our record, over half a million years ago, man was a single species, *Homo erectus*, perhaps already divided into five geographic races or subspecies. *Homo erectus* then evolved into *Homo sapiens* not once but five times, as each subspecies, living in its own territory, passed a critical threshold from a more brutal to a more *sapient* state" (Coon 1962:657).

Coon's hypothesis of modern humans evolving essentially independently from one another five times (Figure 7) was met with a mixed reception on the academic stage. He did find support in figures such as Ernst Mayr (Mayr 1962), but was also fiercely criticized by scientists such as Sherwood Washburn (Washburn 1964) and others (Dobzhansky 1961; Dobzhansky 1963a; Dobzhansky 1963b; Montagu 1963). Coon's work was seized upon by the segregationist movement and used to argue for European supremacy. It was apparent by 1962 and the publication of *The Origin of Races* that this was not a new phenomenon for Coon. In 1950 he stated, "…we have no right to stop working because our material may be dangerous when placed in unskilled hands, any more than atomic physicists should cease their researches for the same reason" (Coon et

al. 1950). With this statement, published only five years after the bombing of Hiroshima and Nagasaki, Coon demonstrated his disregard for the ethical implications of his research.

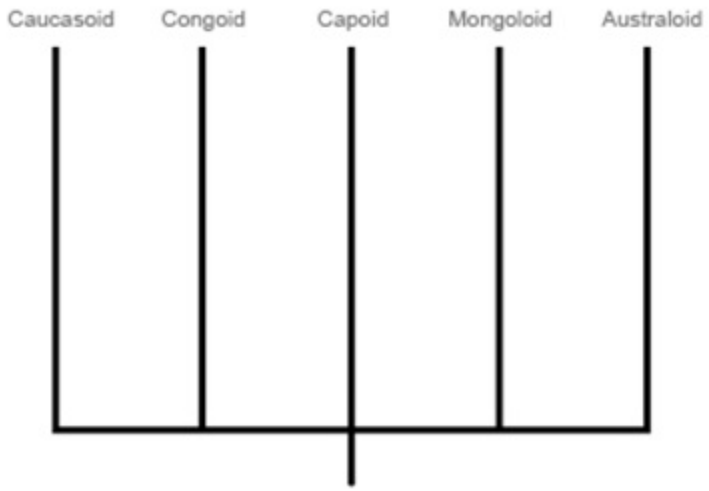

Figure 7. Model of polycentric hominin evolution adapted from Coon (1962:657).

The models created by Weidenreich, and later Coon, were not well received by other anthropologists at the time they were published. The majority opinion by far appeared to support the alternate view of Late Pleistocene hominin evolution where archaic populations did not contribute to and were not direct, sole ancestors of later modern populations (Trinkaus and Shipman 1993). C. Loring Brace was one of the few anthropologists who examined Weidenreich's work and argued against an abrupt morphological and archaeological break between Neandertals and Upper Paleolithic modern humans in Europe, meaning that that Neandertals were ancestral to modern

humans. These conclusions generated controversy in paleoanthropology and the harsh criticism between the two competing theoretical camps negatively impacted communication for decades (Brace 1962; Brace et al. 1964).

The candelabra-like model of hominin evolution (Figure 7) and modern human origins proposed by Coon and Howells' misinterpretation of Weidenreich's work became closely associated with the origins of MRE theory (Templeton 2007). Because of this, the origins of MRE have an unfortunate affiliation with the segregationist movement of the American mid-20th century. With the benefit of hindsight, we now know that Coon's conclusions were deeply and inherently flawed, but their association with the beginnings of MRE cast a long shadow over the further development of this body of theory.

2.4 1980s to Present-Day

In the 1980s, two oppositional bodies of theory were created to interpret the landscape of Late Pleistocene hominin evolution: 1) the Out-of-Africa (OOA) or Replacementist view and 2) the Regional Continuity or Multiregional Evolutionary (MRE) view (Aiello 1993; Stringer and Andrews 1988). The contentious nature of the debate has persisted in certain instances and collaboration has been complicated by persistent miscommunication between the two major camps. Reasons for the continued debate have been examined in detail in the academic literature (Wolpoff et al. 2004; Wolpoff et al. 2000; Wolpoff et al. 2001).

It appears that one of the largest assumptions employed by both sides of the debate is that each body of theory has remained stagnant in the face of continued scientific discoveries. It is very common for opposing camps to take articles describing the hypothetical models of Late Pleistocene hominin evolution from nearly a century ago and assume that current scientists are still operating under those same principles. This misinterpretation seems especially prevalent when the origins of MRE theory are examined. While both OOA and MRE based models certainly do inherit a great deal from previous work, both theoretical concepts have been modified in response to discoveries in the fossil, archaeological, and paleogenetic records. The body of past theoretical publications creates a historical context whereby both modern OOA and MRE can be better understood, but it is an oversight to ignore recent publications from both sides of the debate.

In addition to the two main sides of the debate (OOA and MRE), strict interpretations of which can be viewed as opposite ends of the theoretical continuum, more intermediate models have also been created to bridge the gap between the two sides. Hominin evolution is/was an extremely complex process and the pattern that took place in one geographic area at one time might not necessarily be the same in other areas and at other times. The main intermediate model that will be discussed here is the Assimilation Model (AM), specifically how it addresses Late Pleistocene evolution of Late Neandertals and EMHs. Other derivative models of MRE and OOA, such as the Afro-European sapiens hypothesis (AES), are discussed within the sections for those main bodies of theory.

As previously stated in this section, the fossil record has undergone a great deal of expansion and upheaval since 1980. These changes include both modifications of what we already thought we knew, as well as additions of completely new specimens to our body of knowledge. One of the largest changes to the former of these two categories is encompassed by the increased accuracy of absolute dating methods including, but not limited to, radiocarbon dating and the calibration curve, electron spin resonance (ESR), and uranium/thorium (U/TH). Specimens that were unable to be dated by absolute methods are now accessible by any number of different techniques and, in other cases, specimens have been redated and found to actually belong to different time periods than originally thought. The impact of absolute dating on modern paleoanthropological study cannot be overstated.

One of the best examples of how absolute dating directly impacted interpretations of Late Pleistocene evolution and the origins of modern humans can be seen in the redating of the specimens from the Levant: specifically Amud, Tabun, Kebara, Skhūl, and Qafzeh. For many years it was assumed that the more modern specimens from Skhūl and Qafzeh were younger than the Neandertals recovered from Amud, Tabun, and Kebara, due to pervasive assumptions in paleoanthropology regarding the deterministic nature of hominin evolution. It was commonly believed that hominin morphology changed in a linear manner from more to less robust throughout time. Thus, more gracile "modern" specimens were thought to be younger than more robust archaic looking specimens. A typical interpretation of the Levantine fossil record was that the Neandertaloid group (from Amud and Tabun) inhabited the area first and

the more modern group from Skhūl and Qafzeh came later. The population represented by Skhūl and Qafzeh was also hypothesized to either be: 1) directly descended from Neandertals and ancestral to later fully modern *Homo sapiens* or, 2) be a hybrid population between Neandertals and modern humans (Brace et al. 1964; Keith and McCown 1937; McCown and Keith 1939; Montagu 1947; Weidenreich 1946; Weidenreich 1947a; Weidenreich 1947b).

Prior to the late 1980s, it was believed that the Skhūl/Qafzeh specimens dated to approximately 40 thousand years ago and those from Amud, Tabun, and Kebara dated to greater than 50 thousand years ago. In 1988, the hominin-bearing deposits at Qafzeh were tested with thermoluminescence (TL) and electron spin resonance (ESR) methods on burned flints. The researchers obtained dates that were much older than expected: ~90-100 thousand years ago. These dates were approximately 40 ka older than the then recently dated Neandertal specimens from Kebara, which had been absolutely dated to ~60 thousand years ago. (Schwarcz et al. 1988; Valladas et al. 1988). The reaction to the revised dates was not universally and immediately accepting, especially among prominent proponents of MRE, and the results were criticized both on the basis of the methodology, as well as the implications for hominin evolution in the Levant (Bower 1988; Stringer et al. 1989).

This interpretation of the revised Levantine fossil record was based partially on the assumption that the EMH individuals from the Skhūl site still belonged to a significantly younger era, possibly as young as the previously hypothesized ~40 thousand years ago. This produced a picture where it appeared that EMH moved into the

Levant very early and experienced a long period of contemporaneity and overlap with Neandertals of as little as 20 thousand years ago or as great as 40 thousand years ago based on the previously obtained dates for the Kebara Neandertals. The question of how Neandertal and EMH populations maintained morphological distinctness and apparent stasis (for the EMH group) was of great concern (Bower 1988; Wolpoff 1989). This question was partially answered in 1989, when the dating of the Skhūl EMHs was also revisited with TL and ESR methods. The dates produced by this analysis, 81 ± 15 thousand years ago and 101 ± 12 thousand years ago, fell in line neatly with the information previously obtained on the Qafzeh material. This indicated that the Skhūl and Qafzeh material were both contemporaneous and much older than the documented Neandertal presence in the Levant (Stringer et al. 1989). There was then no apparent evidence for a long period of morphological stability in the Levantine EMH population, though there still existed the possibility of a long period of overlap between the two populations.

Questions regarding the possibility of extended overlap between Levantine Neandertals and EMHs have also been addressed using complimentary archaeological and faunal data. It was discovered that the Skhūl and Qafzeh EMHs, who inhabited the area during OIS 5, were associated with an African biome, while the later-dated Neandertals were not (Tchernov 2002). The implication is that the EMHs of the Levant retreated back into the African Continent or underwent a process of localized extinction when temperatures dropped, which allowed Neandertals to expand into the area with colder-associated fauna (Tchernov 2002).

The preceding Levantine case study demonstrated to paleoanthropologists that the traditional model of deterministic evolution for hominins from robust to gracile in all geographic areas and at all times was truly intellectually dead. And it is quite probable, based on this data, that EMHs and Neandertals never overlapped or came into contact in the Levant. In this particular area and at this particular time period, it appears that a replacement-based model best fits the available evidence. However, this conclusion does not have any bearing on hypothesized evidence of admixture or contact via morphology or archaeology in other geographic regions and at other times.

2.4.1 The Replacement Model and Its Derivatives

By the 1980s, it was commonly accepted by the scientific community that a traditional interpretation of the Presapiens model no longer fit with the hominin fossil record. It was apparent that the available data had disproven the idea that large brains evolved prior to more gracile faces. It had also disproven the hypothesis that there was a deep time scale regarding the origins of fully modern morphology and that evolution had taken place in Europe (Bräuer 1984). Paleoanthropologists began the process of reexamining the fossil record to produce new theories of Late Pleistocene hominin evolution in the Old World. In addition to the fossil record, new lines of evidence were incorporated into the debate, such as ancient DNA (aDNA), increased accuracy in absolute dating methods, calibration of carbon-14 dating, increased reliance on quantitative methods, etc.

Gunter Bräuer sought to completely revise the Presapiens model and, in 1984, published his Afro-European *sapiens*-hypothesis (AES). The AES was first introduced by Bräuer in 1982 at a meeting of the Congrès International de Paléontologie Humaine in Nice, France, and was developed extensively in the early to mid-1980s. Bräuer's work was expansive in examining the Middle and Upper Pleistocene fossil record from Africa and incorporating that with what was also known about the revised record for Europe and Asia. The AES postulates that it was unlikely that modern humans first appeared in Northern Africa. Instead, it was thought that an archaic population with Neandertal characteristics inhabited Northern Africa until at ~30 ka bp. This was largely based on interpretations of the Mugharet el' Aliya and Jebel Irhoud specimens. The AES also proposes that EMHs first appeared in Eastern or Southern Africa and that, by the Late UP, had spread across most of the African Continent. The model also proposes that EMHs did not leave Africa until the LGM, or Würm glaciation, after which they replaced and possibly experienced some limited admixture with the archaic populations they may have encountered (Bräuer 1984).

As thorough as Bräuer's work (1984) was, the AES was quickly disproven in the next decade. Each of the previous three tenets of the model listed in the previous paragraph has been disproven or was show to be based on evidence that has been reinterpreted or heavily revised. The first and second propositions of the AES (that EMHs did not evolve in Northern Africa because there was an existing population of Neandertals in that area and thus EMHs first appeared in Southern or Eastern Africa) are based on the hypothesis that fossils from sites like Jebel Irhoud and Mugharet el' Aliya

can be classified as Neandertals. North African fossils, such as those from Jebel Irhoud, were originally thought to be Neandertals based on their higher levels of morphological robusticity. In addition, the presence of parasagittal lateral bulging was noted, which is also seen in European Neandertals (Bruner and Pearson 2013). However, some of these North African specimens have since been reclassified as representative of EMHs. This reclassification is based on their early date of ~160 thousand years ago as well as a detailed assessment of their developmental patterns that group with modern humans rather than Neandertals (Smith et al. 2007). Many paleoanthropologists have argued convincingly that the presence of Neandertal autapormophies, traits unique to Neandertals, have not been documented on the Jebel Irhoud group (Hublin 2001). The traits previously argued to be indicative of Neandertal affinity are now thought to be symplesiomorphic in nature (Bruner and Pearson 2013; Hublin 2001).

The final tenet of the AES proposed by Bräuer in 1984 is that EMHs did not exit the African Continent until very late, during the time of the Last Glacial Maximum (LGM) (Bräuer 1984). This hypothesis was based partially on the then accepted dates of the Skhūl and Qafzeh specimens and their relationship with the Levantine Neandertals. Tenet #3 does make sense if the Skhūl and Qafzeh EMHs were younger than the Neandertals from the same geographic area. At the time that Bräuer created the AES, the Levantine fossil chronology had not yet been revised. The AES chronological scheme was also based on the assumption that no EMH fossils could be documented in Europe until during the LGM. Revised dating of European EMHs has also found this

interpretation to be incorrect, with some of the oldest documented EMH fossil dated to ~39 ky cal BP (Trinkaus 2005; Trinkaus et al. 2003).

After the evidence demonstrated that the AES needed to be greatly modified, Bräuer published a revision of the model in 1992. This version became known as the African Hybridization and Replacement model (AHR). The details of the AES were modified to fit the current interpretation of the chronology of the hominin fossil record, but the AHR model kept the hypothesis that EMH populations exiting Africa largely replaced the archaic populations they came into contact with. The AHR does continue to allow for some limited admixture between modern and archaic populations in different areas of the Old World, but that gene flow is seen as not extremely significant in the formation of later modern populations (Aiello 1993).

Another replacement-based model for Late Pleistocene evolution was also being generated during the late 1980s and early 1990s. In 1984 Chris Stringer proposed the first version of what would become known as the Out of Africa (OOA) model (Stringer 1992). This model is also called the Recent African Origins (RAO), Recent Single-Origins Hypothesis (RSOH), or Out of Africa II (OOA II) in the paleoanthropological literature (Smith et al. 1989). One of the main differences between the RAO and the AES/AHR is that, in the RAO, admixture between archaic and incoming modern populations is hypothesized not to have occurred at all (Stringer 1992). On the continuum of models of Late Pleistocene hominin evolution from replacement to continuity, the RAO is the most extreme of the replacement-based models. The original formulation of the RAO model set the African Continent as the place of origin for the

evolution of modern humans (Stringer and Andrews 1988; Stringer 1992), though it does not specify a specific region of that continent as does the original version of the AES (Bräuer 1984).

> "…the single origin model assumes that there was a relatively recent common ancestral population for *Homo sapiens* which already displayed most of the anatomical characters shared by living people. Proponents of this model have proposed Africa as the probable continent of origin of *Homo sapiens*, with an origin for the species during the early part of the late Pleistocene, followed by an initiation of African regional differentiation, subsequent radiation from Africa, and final establishment of modern regional characteristics outside of Africa" (Stringer and Andrews 1988:1263).

One of the most controversial tenets of the RAO model proposed by Stringer and Andrews is the reliance on replacement in the formation of EMH populations across the Old World. Under the RAO, EMHs moved out of Africa in the Late Pleistocene and either did not encounter archaic populations or replaced them without admixture if they did come into contact. Stringer and Andrews (1988) state, "Transitional fossils would not occur outside the African area of origin, and population replacement would represent the mode of establishment of *Homo sapiens* in other areas."

The authors of the original version of the RAO argued strongly that there is no genetic nor morphological evidence of gene flow between EMHs and archaic populations anywhere in the world. With regards to their arguments on Europe specifically, all fossils that paleoanthropologists had previously interpreted as displaying

evidence of transitional morphology were instead argued to not display any morphological indicators of interbreeding. Instead, any archaic traits found were typically interpreted instead as shared ancestral traits. The modernity and relative gracility of the first European EMHs was emphasized and the European fossil record interpreted as showing a distinct break between Neandertal and EMHs. The origins of modern humans by RAO was treated as a speciation event (Aiello 1993; Stringer and Andrews 1988; Stringer 1992).

Stringer & Andrews' (1988) original publication concisely laid out the predictions for the fossil record if RAO were the method by which Europe was peopled by modern humans. In addition, the RAO proposed a major shift in population dynamics during the Late Pleistocene. Rather than long periods of continuity in isolated geographic areas dating to when those regions were first peopled by ancestral populations in the Early Pleistocene (specifically during the Calabrian stage of the Pleistocene), the RAO proposed that a sharp break was observable in the fossil, archaeological, and genetic records. The proposed pattern is illustrated in Figure 8, which includes the original caption (Stringer 1992).

Both ROA and the AHR have proven to be very popular among paleoanthropologists and these two hypothetical models have been continuously tested with new fossil and other data as they appear. It is not uncommon for research questions to be approached with the assumption that the ROA or AHR has already been "proven" correct. However, this approach should be taken with extreme caution. Paleoanthropology is governed by the same laws as all scientific studies in which a

hypothesis can only be disproven or fail to be disproven. The modern versions of replacement-based models certainly offer a compelling hypothesis on the interpretation of the hominin fossil record and, given the nature of paleoanthropological study, the debate between the appropriateness of replacement and MRE-based models will not wane in the future.

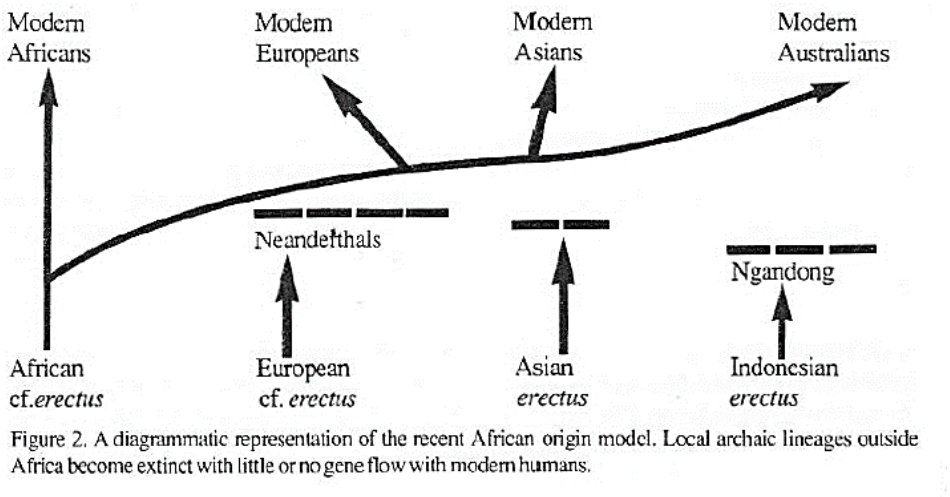

Figure 2. A diagrammatic representation of the recent African origin model. Local archaic lineages outside Africa become extinct with little or no gene flow with modern humans.

Figure 8. Stringer's illustration of the RAO (1992:12).

2.4.2 Multiregional Evolution (MRE) and Its Derivatives

In the early 1980s, during the same time as the development of the AES and RAO, paleoanthropologists were also developing hypotheses of Late Pleistocene hominin evolution that argued for the importance of gene flow and regional morphological continuity. As with the origins of Weidenreich's model, the origins of modern MRE theory were formed using data from Asia rather than Europe. In 1981,

Thorne and Wolpoff reported that there appeared to be evidence of morphological continuity between the reconstructed Sangiran 17 specimen discovered in Indonesia and male individuals from the Australian site of Kow Swamp. While this possible continuity had been noted in the 1940s by Weidenreich, Thorne and Wolpoff set out to metrically quantify the similarities and possible relationship. The authors argue that it is not the presence of any one morphological trait, but the overall pattern and frequency of traits in both Indonesian *Homo erectus* and modern Australo-Asian specimens that indicates some form of contribution (i.e. gene flow) by the archaic population to later modern populations from the same area. Contrary to some later interpretations of their work, Thorne and Wolpoff never argue for an isolated or region-specific evolution of *Homo erectus* into later modern humans. For example, "Regional continuity need not be considered indicative of prolonged genetic isolation…Indeed, the grade differences between Sangiran 17 and the Kow Swamp group outweigh the similarities we regard as due to morphological clade, and by and large these differences are evolutionary trends that were worldwide." The overall morphological pattern observed in the fossil evidence is one where the center of the population displays higher levels of morphological variability than the populations at the geographic edges of their range (Thorne and Wolpoff 1981).

Based on their analysis of the SE Asian evidence, Thorne and Wolpoff (1981) proposed a "Center and Edge" model (C&E) for the creation of the pattern seen in the morphology of *Homo erectus* through modern humans. The hypothetical model for the development of modern humans under C&E as proposed by Thorne and Wolpoff states

that *Homo erectus* evolved in East Africa and was the first hominin group to migrate out of the African continent, dispersing into the geographic peripheries of Asia and Europe. After this large scale migration, clinal differences were established among hominin populations in different geographic regions and the hominin populations at the geographic peripheries tend to show a more morphologically homogenous pattern. The long term morphological continuity and stability is created and maintained by a continuous level of recurrent gene flow radiating from the geographic center to the edge populations (Thorne and Wolpoff 1981; Wolpoff et al. 1984).

By the 1980s, it had become apparent that the geographic origin of the hominin lineage was in Africa rather than elsewhere in the Old World. The fossil evidence collected from Africa had, by that point, made it increasingly apparent that Euro-centric unilineal hypotheses of hominin evolution were no longer tenable. The question that began to be asked in the 1980s was whether or not there was evidence of a second major wave of migration out of Africa significantly later than the first migration of *Homo erectus* into the rest of the Old World. This second wave was proposed by RAO proponents to have consisted of EMH populations that swept through and completely replaced any remaining archaic populations they might have encountered without the exchange of genetic material (Harvati et al. 2004; Klein 2003). These hypotheses ran counter to the interpretations of the fossil record in Europe and elsewhere by proponents of models that incorporated gene flow. When MRE was applied to the European Fossil record to interpret the relationship between Neandertals and EMHs, proponents of this

model concluded that there was ample evidence to conclude that Neandertals contributed to later modern populations.

> "Do modern Europeans have a single unique African ancestry, or are European Neandertals among their ancestors? We show here that *the hypothesis that Neandertals are a significant part of the ancestry of Europeans* is well supported…To be clear, 'significant' in this context means that Neandertal are among the ancestors of later Europeans, not that Neandertals are the unique or only ancestors of later Europeans…that Neandertals provided enough of a genetic contribution for their traits to be readily identifiable in later Europeans, and some even found in Europeans today" (Wolpoff et al. 2004).

Through the 1980s and 1990s, a series of opposing articles were published in the academic literature and the two theoretical camps of MRE and RAO became increasingly polarized (Aiello 1993; Thorne and Wolpoff 1981; Wolpoff et al. 2000). While modern MRE was developed specifically to explain the patterns observed in the East Asian fossil evidence, the transition from Neandertals to EMH in Europe is often viewed as a "stronghold" of MRE theory by critics (Cavalli-Sforza 1998). MRE traditionally emphasizes gene flow and regional continuity (i.e., admixture with archaic populations) to a large degree. MRE proposes instead that, once populations were established throughout the Old World, all populations experienced at least some small level of gene flow with adjacent populations and thus that a traditional speciation event was not behind the appearance of Neandertals and later modern humans. In fact, in some versions of MRE it has been proposed that all populations of hominins since *Homo*

erectus sensu lato can be subsumed under a single species hypothesis (Wolpoff 1984; Wolpoff et al. 2000).

Part of the contentious nature of the debates concerning MRE versus RAO-based models is due to repeated misinterpretation of the nature of MRE and its subsidiary models. The models that proponents of replacement-based hypotheses were critiquing were typically more methodologically similar to the predecessors of modern MRE created in the earlier parts of the 20th century (Relethford 2008; Relethford 1998; Templeton 2007; Wolpoff et al. 2000). By the 1980s and 1990s, those models were 40 or 50 years past their initial formation and were in the process of being updated (as were the replacement-based models) to take into account the immense changes the fossil and archaeological record had seen in the interim. The development of anthropological and evolutionary theory as it pertains to hominins has never stagnated or enjoyed a long period of true stasis. While it is incredibly important to understand the theories from which current evolutionary models were developed, it is a mistake to make the supposition that previous models can stand in place of what the current models hypothesize.

MRE readily acknowledges the high levels of complexity that may have occurred over the course of hominin history during the Pleistocene. Rather than proposing one simple answer for the origins of modern humans, as does RAO, instead MRE proposes that there were many factors involved in hominin evolution and the pattern seen in one region at one time does not imply that other areas and other times have the same evolutionary pattern (Smith et al. 1989; Thorne and Wolpoff 1981; Wolpoff 1984;

Wolpoff et al. 1984). This incredible complexity, while perhaps a more appropriate way to frame evolutionary hypotheses, has also added to the confusion in the literature as to the specific structure of MRE.

As a result of the changing evidence, including the polarization of MRE and replacement-based models in the 1980s, an ever increasingly detailed fossil and archaeological record, and the development of more accurate ancient genetic analyses, other "weaker" theoretical models were developed. The AES and the AHR, as previously discussed, grew out of strict replacement-based models. The Assimilation Model (AM) grew out of the multiregional side of the theoretical spectrum.

In the AM, modern humans are hypothesized to have evolved in Eastern Africa at a fairly recent date and then migrated out of the African Continent, perhaps in successive or multiple waves, where they encountered extant populations of archaic hominins in varying densities across the Old World. These archaic populations were then absorbed into EMH populations by a process of admixture. However, the levels of gene flow between archaic and modern populations may have varied widely between different geographic regions. The major theoretical themes of the AM do not differ widely from the AES and weaker versions of the RAO. However, the AM postulates that the gene flow that occurred between archaic and modern groups was significant despite the fact that absolute levels of admixture may have been quite small. The AM differs from MRE mainly in the levels of gene flow that are hypothesized to have occurred (Smith et al. 1989; Smith et al. 2012).

The AM predicts that evidence of the assimilation of archaic populations should be found in later modern populations, but that the degree of that evidence is less than is predicted by the strict modern MRE. This evidence of continuity between archaic and modern groups might also vary in different geographic regions (Smith et al. 2012). Evidence of contact between archaic hominins and incoming EMH populations could also be seen in the archaeological record under the theoretical constraints of the AM. Here this might take the form of transitional industries between technocomplexes associated with the two groups.

The AM had a poor reception in the 1990s and received very little support until the mid-2000s (Gibbons 2011). Increased support of the AM was gained in the academic literature following morphological analyses of specimens such as Oase (Trinkaus et al. 2003; Zilhão et al. 2007) and the more controversial Lagar Velho I (Duarte et al. 1999). The research into aDNA evidence for European pre-history specifically has been used to argue both for and against the AM and MRE models (Holliday 2014; Stringer 2014). When analyzing the data from Europe, Trinkaus stated, "…the ubiquitous evidence among early modern humans for some level of admixture with regional late archaic human groups outside of eastern Africa indicates that assimilation was neither rare nor trivial. It was the geographically dominant pattern" (2005).

2.5 Summary

The two diametrically opposed viewpoints between RAO and MRE models of Late Pleistocene hominin evolution that developed in the 1980s and 1990s were not

unique in the history of paleoanthropology. From paleoanthropology's infancy in the late 19th and early 20th centuries up to the present date, the field has generally formed itself into two oppositional bodies of theory especially in regards to the origin of modern humans. These two camps can be described over the past 125 years as either replacementist or those models that are accepting of either gene flow/archaic contribution to later modern populations.

The tenants of replacementist models have changed less dramatically over the course of 100 years than has the body of gene flow/admixture theory and statements made by scholars such as Marcellin Boule 100 years ago are remarkably similar to some of the arguments put forth in modern paleoanthropological studies. However little some of the arguments have changed in replacement-based models, the theoretical reasons for the exclusion of archaic populations as even tangentially ancestral to modern humans has changed. When paleoanthropology was in its beginnings as a discipline, it was commonly believed that modern humans needed to present a pure lineage with no contribution from other populations for religious reasons (Trinkaus and Shipman 1993). The most striking difference between the two camps is how they treat the possible contributions of archaic populations to later populations. The MRE and AM camp says that this contribution, even if small, was important and mattered in the grand scheme of ancient population dynamics and the evolution of humans throughout time. The RAO and AES camp says that, if this contribution happened, it was so small as to essentially be insignificant in the creation of modern human populations around the globe.

As applied to this study, these two types of models have distinct implications for Late Pleistocene hominin behavior in Europe. Replacement-based models hypothesize that Late Neandertals and EMHs experienced no or minimal amounts of admixture if/when they came into contact. Under the basic tenets of replacementist models these two populations may or may not have overlapped geographically, thus models investigating the exact nature of Late Pleistocene population dynamics in Europe can imply discrete or overlapping fundamental niche parameters and still fit under the umbrella of replacement based models. However, models that hypothesize or imply separate niches, and thus discrete areas of suitable habitat for Neandertals and EMHs, can always be classed as replacement-based. The Ebro Frontier Model (EFM), hypothesizes that there was an eco-geographic barrier that separated Late Neandertals and EMHs in Iberia until approximately 30 thousand years ago. The implication is that the fundamental niches of these two populations in Iberia remained discrete until immediately prior to Neandertal extinction. In contrast, models of Late Pleistocene evolution that place more importance on gene flow between archaic and modern human groups imply some level of niche and geographic overlap. This hypothesized overlap is necessary to the Assimilation Model (AM) and Multiregional Evolution (MRE) in order to facilitate admixture between hominin populations, and as specifically addressed by this dissertation, European Late Neandertals and EMHs.

As this review shows, the implications for the nature of Late Neandertal and EMH population dynamics, interaction, and ecology for replacement-based and admixture-tolerant models are often left unstated and untested. However, once they are

examined closely, testable hypotheses concerning these topics become apparent. This dissertation takes a novel and multidisciplinary approach to addressing these holes in our current body of knowledge.

3. THE EBRO FRONTIER MODEL AND ECOLOGICAL NICHE MODELING (ENM)

The theories of hominin evolution discussed in Section 2 propose specific behaviors for Neandertals and EMHs during the Late Pleistocene in Europe. This body of theory has generated many region-specific hypotheses for Neandertal late survival and extinction as well as the nature of their possible interaction with incoming EMHs. One of the most discussed of these hypotheses is the Ebro Frontier Model (EFM). The EFM is of interest to this project in particular due to the fact that it proposes an ecological barrier as an explanation for the pattern and mode of Late Pleistocene evolution in Iberia. Despite methodological constraints that forced this dissertation to expand its analysis and sample beyond the borders of the Iberian Peninsula, a discussion of the EFM benefits the project as the ecological mechanism it proposes could be applied to other geographic areas and other time periods. This project utilizes novel methods to examine whether the Ebro Frontier or other ecological barriers across Europe can be identified. This section includes a detailed discussion of the Ebro Frontier Model, the history of ecological niche modeling (ENM) in anthropological study, and the theoretical constraints of ENM research.

3.1 The Ebro Frontier Model

The Ebro Frontier Model was first described in the anthropological literature by Zilhão (1997) and quickly became a topic of intense debate in paleoanthropology and

Paleolithic archaeology (Daura et al. 2013; Duarte et al. 1999; Jöris et al. 2003; Maroto et al. 2012; Vaquero et al. 2006a; Vaquero et al. 2006b; Walker et al. 2008; Wood et al. 2014; Wood et al. 2013; Zilhao 1997; Zilhão 2000; Zilhão 2009). Prior to its debut in the literature, Zilhão proposed the model in October of 1991 at the Madrid Conference on the Origins of Anatomically Modern Humans. The model is based on two perceived observations: 1) that the Mousterian industry appeared to have survived in southern Spain (Valencia, Andalucía, and Gibraltar, etc.) until approximately 28-30 ky cal BP, and 2) that the Upper Paleolithic first appeared north of the Ebro River Valley (Figure 9) and does not move south of that geographic landmark until approximately 30 ky cal BP. (Finlayson et al. 2006; Maroto et al. 1996; Villaverde and Fumanal 1990; Zilhão 2000).

The Ebro River is located approximately 100 kilometers (62 miles) south of the Pyrenees Mountains and runs east-southeast across northern Spain where it drains into the Balearic Sea, a section of the Mediterranean Sea (Figure 9). Under the model's tenets, EMHs are proposed to have arrived in the northern portion of Iberia at approximately 35 ky cal BP. The Ebro River is hypothesized to have remained a meaningful ecological barrier or frontier to both late surviving Neandertals and EMHs for approximately 5 to 10 thousand years. After 30 ky cal BP, some change is proposed to have occurred and the Ebro River Valley no longer acted as an impermeable ecological frontier. Immediately following this change, EMHs entered the southern portion of the Iberian Peninsula where they came into contact with the last of the Iberian Neandertals. Neandertal extinction in Iberia is then hypothesized to have occurred by a

process of competitive exclusion, perhaps aided by admixture and genetic swamping (Zilhao 1997; Zilhão 2000; Zilhão 2009; Zilhão and Pettitt 2006).

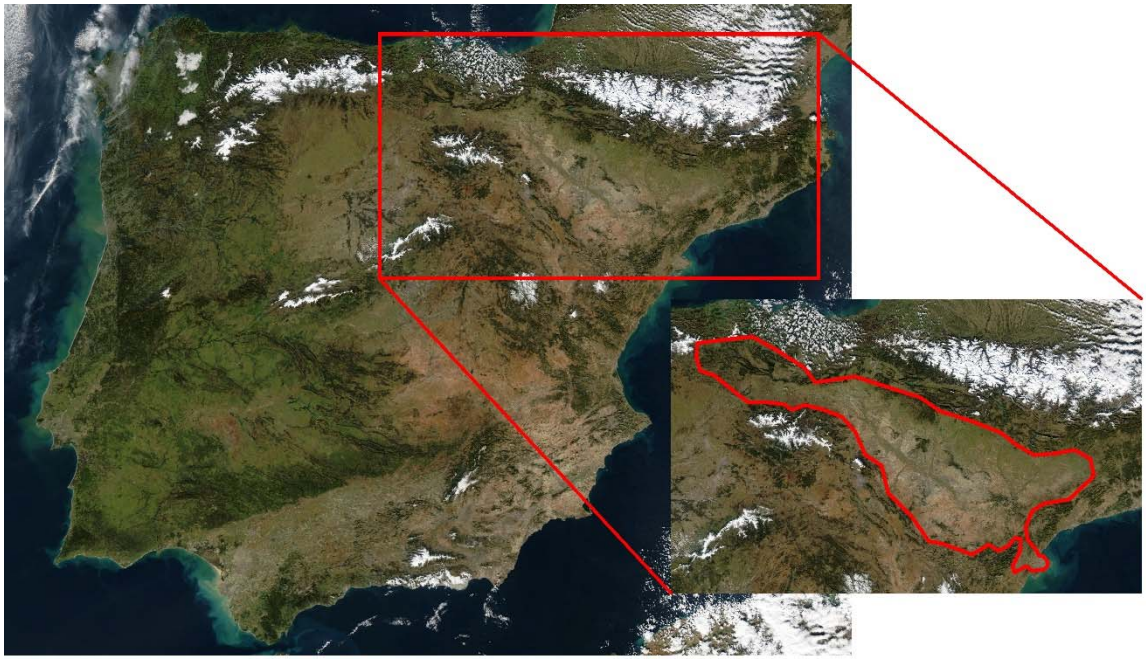

Figure 9. The Iberian Peninsula with a rough outline of the Ebro River Valley. Modified from an aerial photograph courtesy of the National Aeronautics and Space Administration.

The majority of the critique of the Ebro Frontier model concerns the dating and geographic location of some archaeological sites. The model was created to explain the perceived temporal and geographic distribution of late MP and early UP sites in Iberia and was built on the supposition of the late appearance of fully UP technologies south of the Ebro River. The distribution of these archaeological sites has been used to argue that southern Iberia acted as a refugium for late surviving Neandertals while EMHs were prevented from accessing that area until relatively late (Zilhao 1997; Zilhão 2000; Zilhão

2009). However, the proposed date of the oldest sites identified as Upper Paleolithic south of the Ebro River has undergone much debate and revision in the last 20 years (Jöris et al. 2003; Maroto et al. 2012; Wood et al. 2014; Wood et al. 2013).

The debate surrounding the specific transition from Middle Paleolithic (MP) to Upper Paleolithic (UP) in Iberia is complicated by factors regarding the ambiguity of the carbon-14 (14C) dating method used to absolutely date these sites. The proposed temporal range pertinent to the Ebro Frontier Model (EFM) is close to the effective limits of 14C and calibration methods (Anikovich et al. 2007). Any small amount of contamination with modern carbon can throw off the resulting dates by at least several thousand years, making them appear younger than they actually were (d'Errico and Sánchez Goñi 2003; Jöris et al. 2003; Wood et al. 2013).

Also, the dating of some MP sites in Portugal has been found to be suspect due to low levels of collagen or uranium, which can greatly impact the ability to determine accurate 14C dates (Zilhão 2000). The site with the most reliable dates from this period is Cueva Anton, placed at circa 38 – 32 ky cal BP, but the charcoal that has been used for dating this site is not directly associated with the archaeological remains and the data has not yet been fully published. The archaeological assemblage in the absolutely dated level has only been provisionally classified as MP, based on the size of the assemblage and lack of diagnostic UP artifacts (Wood et al. 2013).

Sites north of the Ebro River containing MP tools, such as El Esquilleu, Ermitons, La Güelga, and Cova Gran, have now been assigned more recent dates than previously accepted. These new dates fall later than those expected from the Ebro

Frontier Model. This may indicate that the terminal MP found north of the Ebro River occurred later than was previously thought (Maroto et al. 2012; Vaquero et al. 2006b). The reverse also appears to be true: sites with UP material south of the Ebro River, such as the caves of Bajondillo and Foradada, have UP occupations that have been re-dated to the time period preceding the benchmark proposed by the Ebro Frontier Model (Maroto et al. 2012). If the assumption is made that tool types equal population or species level differences, the above re-dated sites indicate that Neandertal populations continued to exist north of the Ebro River until after 35 ky cal BP and that EMH populations were present south of the river prior to 30 ky cal BP (Finlayson et al. 2008). There appears to have been less of an abrupt transition from Middle to Upper Paleolithic technocomplexes than was previously believed (Maroto et al. 2012; Pike-Tay et al. 1999; Vega et al. 1999; Wood et al. 2013).

As discussed above, the Ebro Frontier Model began as a way to explain the perceived geographic and temporal distribution of Middle and Upper Paleolithic sites on the Iberian Peninsula. Because the ratio of sites that have produced hominin remains in comparison to total number of archaeological sites is quite small, archaeological data has been the primary source of information used to support and critique the model. The relative paucity of hominin remains from the pertinent time periods has been a complicating factor for previous research. Ideally, samples of absolutely dated, morphologically diagnostic hominin remains in close association with diagnostic lithic artifacts for both Middle and Upper Paleolithic type industries could be used to test the assumptions used in the creation of the Ebro Frontier Model, as well as other

archaeologically-based hypotheses of Neandertal extinction. Unfortunately, only a few diagnostic hominin remains from the Iberian Peninsula and the rest of Europe dating to the time period of interest have been recovered and described in peer-reviewed literature (Duarte et al. 1999). This makes every hominin specimen that can be confidently classified and dated to the time period during and just prior to Neandertal extinction extremely important to the discussion of recent hominin evolution in Western and Central Europe.

While the number of sites producing morphologically diagnostic Neandertal remains for the time period of this study (43.3 – 36.5 ky cal BP) is relatively small, no previous studies have separated out this sample from other archaeological sites when investigating Neandertal and early modern human population dynamics during the Late Pleistocene. This sample of sites that have produced diagnostic Neandertal remains is a more theoretically conservative one for modeling Neandertal presence and the extent of their suitable habitat since it avoids the debate concerning using stone tools to act as proxies for human populations. After a review of the published peer-review literature, only 17 sites that have produced well-dated Neandertal remains for the time period of this study were identified by the author of this dissertation, while there are 32 additional sites with well-dated Middle Paleolithic layers and 39 sites with Upper Paleolithic material. These will be discussed in greater detail in Section 4.

3.1.1 Technocomplexes as Proxies for Presence

The Ebro Frontier Model is based on several assumptions that have not been adequately tested. One of the largest of these is that lithic artifacts assigned to cultural technocomplexes can stand as proxies for populational presence. Specifically, Neandertals have been assumed to be the exclusive creators of Mousterian and those industries typically considered to be MP-derived, i.e., Châtelperronian, Uluzzian, and Bohunician. EMHs are assumed to have been the exclusive creators of UP industries, such as Early Aurignacian, Aurignacian, and Gravettian (Carbonell et al. 2000; Maroto et al. 1996; Maroto et al. 2012; Zilhao 1997; Zilhão 1998; Zilhão 2000; Zilhão 2001; Zilhão 2009). However, the equation of lithic technocomplexes with population or species level differences has been called into question (Bar-Yosef and Belfer-Cohen 2001). Unless diagnostic hominin remains have been found in direct association with artifacts considered diagnostic to the lithic industries in question, it is very difficult to make concrete assessments about which population created them.

Another theoretical assumption of the Ebro Frontier Model is the identification of MP sites based on the ***absence*** of certain types of stone tools, rather than the positive identification of diagnostic MP artifacts, such as Levalloisian points. If a site contains no blades, bone artifacts, and no evidence of art or personal adornment, it is typically classified as MP and thus Neandertal in origin (d'Errico and Sánchez Goñi 2003; Maroto et al. 2012). Each site must be evaluated for the identification of diagnostic artifacts and information on dating.

3.1.2 The Identification of Ecological Frontiers

The Ebro Frontier Model (EFM) proposes specific features that impact Late Pleistocene hominin evolution in Iberia. One of the most central to this model is the proposed presence of an ecological barrier found in northern Iberia at the Ebro River Valley. A meaningful ecological barrier, as described by the EFM, is one that would prevent populations from moving through or past it to other potentially suitable habitats (Zilhão 2000). In the ecological and biological literature, this concept is known as a biogeographic frontier. Biogeographic barriers have commonly been proposed in all parts of the world. A few select studies in ecology using genetic testing and ENM methods are pertinent to the conversation created when evaluating the major tenets of the EFM. This previous work, discussed below, evaluates the validity of other geographic features commonly hypothesized to have acted as biogeographic frontiers to animal and plant species in the past (during the Last Glacial Maximum, LGM) and during the present: the Pyrenees Mountains (Hewitt 2001) and the Strait of Gibraltar (Fritz et al. 2005; Jaramillo-Correa et al. 2010). Though these studies do not directly address the time period of interest to the Ebro Frontier Model (EFM) and to this dissertation, they are still important as the processes that acted on these species during the LGM and now should give us insight on how these same processes might have affected Late Neandertals and EMHs from 43.3 to 36.5 ky cal BP.

The Pyrenees Mountains have been proposed as a possible biogeographic frontier for other large-bodied, highly mobile mammalian species. However, genetic studies with large mammals show that the Pyrenees Mountains were less of a biogeographic barrier

after the Last Glacial Maximum (LGM) (approximately 26.5 to 18 ky cal BP) than the Alps. Evidence shows higher percentages of brown bear (*Ursus arctos*) recolonization of Europe from Iberia than the Alps during the post-glacial LGM period (Hewitt 2001). This indicates that brown bears had an easier time moving across a landscape that included the Ebro River Valley and Pyrenees Mountains. In addition, if these geographic features did not act as barriers for brown bears, there should be no reason why they should act as a barrier to other large bodied mammals, such as hominins, during the LGM.

Recent work in ecology with terrestrial plants and animals has focused on the use of genetics to test whether or not proposed biogeographic barriers prevented admixture. Studies of Mediterranean conifers (various species) and Spanish pond turtles (*Mauremys leprosa*) found that there was no genetic evidence to support the idea that the Strait of Gibraltar acted as a ecologic frontier for these organisms (Fritz et al. 2005; Jaramillo-Correa et al. 2010). These two modern organisms have distributions that cover southern Europe and North Africa, so studies looking for genetic breaks would be ideal in testing for the presence of frontiers.

3.2 Previous Anthropological Studies Using ENM Techniques

The Ebro Frontier Model (EFM) makes specific hypotheses about the presence of a biogeographic frontier at the Ebro River Valley and the predictions the frontier has for the population dynamics of Late Neandertals and EMHs in Iberia. If there was a biogeographic frontier that existed at the time and place the model proposes, then these

two hominin populations would have been prevented from coming into contact with one another until the time just prior to the disappearance of Neandertals from the fossil record. This dissertation addresses these hypotheses and predictions created by the Ebro Frontier Model (EFM) not only on the Iberian Peninsula, but throughout Western and Central Europe. Previous work in anthropology that is pertinent to this discussion has focused on using archaeological, rather than fossil, data (Banks et al. 2008b). In addition, some of these previous studies have focused largely on examining the interactions between sub-populations of modern humans as defined by archaeological technocomplexes. For example, examining the geographic extent of the suitable habitat for the populations that created Solutrean versus Epigravettian tools, both of which were created by anatomically modern humans (AMHs) in Europe (Banks et al. 2008c).

Many anthropological studies have not used a traditional ecological definition for the term "niche." The adaptation of traditional ENM concepts for use with anthropological samples was originally called eco-cultural niche modeling (ECNM). ECNM is a set of analytical tools derived from multiple disciplines including evolutionary ecology, biology, ENM, and Geographic Information Systems (GIS). It was developed in order to predict the distribution of archaeological cultures and technocomplexes and was designed at two National Science Foundation and European Science Foundation workshops in 2004 and 2005 (Banks et al. 2006).

ECNM is centered on the assumptions that archaeological cultures and technocomplexes act like faunal species and that industries such as the Mousterian or Aurignacian have a one-to-one ratio with their hypothesized creators. These assumptions

allow researchers to take location data (latitude and longitude) for sites designated as belonging to a certain archaeological culture, perform an ENM analysis, and create maps of the potential distributions. Multiple "species" of archaeological cultures may be analyzed at the same time in order to compare possible areas of geographic overlap or exclusivity. The results are then tested to determine if the resulting models are able to predict known test points at a better than random rate (Banks et al. 2006).

In essence, ECNM takes a non-biological dataset and forces it to conform to a modeling system that is geared toward analyzing biological species and populations. The assumption that technocomplexes share a one-to-one correlative relationship with their creators' populational affiliation has not been adequately tested for post-50 ky cal BP Europe. This could be a potential source of noise in the results of studies using ENM techniques and archaeological presence-points. By including the three different samples and testing strategies mentioned in the introduction, this study seeks to address the theoretical implications inherent in assuming relationships between lithic tool types and populations.

Previous ECNM work in anthropology has been produced by Banks and colleagues (Antunes et al. 2014; Banks et al. 2011; Banks et al. 2008a; Banks et al. 2008b; Banks et al. 2008c; Banks et al. 2013a; Banks et al. 2013b; Banks et al. 2009). Of three studies published in 2008, two focus entirely on archaeological data during the Pre-H4, H4, and Post-H4, as well as the LGM (Banks et al. 2008b; Banks et al. 2008c) and one on reconstructing the possible distribution of two common prey species found at archaeological sites during the LGM: caribou (*Rangifer tarandus*) and red deer (*Cervus*

elaphus) (Banks et al. 2008a). Using archaeological samples, two other studies were published by the group in 2009 and 2011 (Banks et al. 2011; Banks et al. 2009) constructing niche predictions for the LGM. Only one other study by the group focusing on archaeological samples in the Pre-H4, H4, and Post-H4 was published in 2013 (Banks et al. 2013a; Banks et al. 2013b). This background will discuss the two studies completed using reconstructions surrounding H4, as they have direct applicability to this project.

The 2008 study by Banks and colleagues argued for competitive exclusion as the driving force behind Neandertal extinction. In the study, sites producing exclusively artifacts and those that produced hominin fossils (in addition to lithic artifacts) are pooled for the analysis. All sites were absolutely dated. The Pre-H4 MP sample contains only three locations that have produced diagnostic Neandertal remains: El Sidrón, La Quina, and Mezmaiskaya. Gruta do Oliveira, also included in the Pre-H4 MP sample, has produced some fragmentary, non-diagnostic hominin remains traditionally classified as Neandertal in origin. No locations in the H4 MP sample that have produced hominin remains, diagnostic or otherwise, were included. Gruta do Oliveira is the only site having produced hominin remains (though fragmentary and undiagnostic) that is included in the Post-H4 MP sample. (Banks et al. 2008b).

With this mainly archaeological sample, the study concludes that there was support for the Ebro Frontier Model shown in the predictive maps for the EMH Pre-H4 UP and EMH H4 UP tests. The southwestern corner of the Iberian Peninsula is shown as not having the presence of environmental variables associated with those samples.

(Banks et al. 2008b). However, this apparent barrier is south of the Ebro River Valley, beneath the Sistema Iberico Mountains and the Meseta Central plateau. In addition, the predictions generated for the MP Pre-H4, H4, and Post-H4 all predict areas of probable Neandertal presence north of the Ebro River Valley.

Banks, d'Errico, and Zilhão's 2013 study using GARP and Maxent also focused exclusively on archaeological samples for the Pre-H4 and H4 Proto-Aurignacian and Early Aurignacian technocomplexes (classified as UP industries). All sites were absolutely dated. Many more presence points were used here than were used in the previous 2008 study due to an increase in research and work with absolute dating of sites (Banks et al. 2013a). The same blank area of absence south of the Sistema Iberico and Meseta Central seen in the Pre-H4 and H4 of the previous study is also seen in the GARP results of this study.

As demonstrated above, previous work using ENM methods with anthropological samples has been based on the use of lithics to stand as proxies for populational presence. However, this assumption has not yet been adequately tested. This project is designed to examine the validity of this assumption, as well as examine the geographic patterning and areas of overlap of correlated environmental variables for Neandertal, MP, and UP sites.

Anthropologists have become increasingly interested in qualitatively describing and quantifying Neandertal and EMH niches. However, this conversation is complicated by an inconsistent vocabulary in which the word "niche" often is defined in many different ways. Research into hominin niches has included examination of environmental

variables (Antunes et al. 2014; Banks et al. 2011; Banks et al. 2008b; Banks et al. 2013a; Banks et al. 2006; Banks et al. 2009), isotopic and archaeological analyses of diet breadth (Bocherens et al. 2005; Drucker and Bocherens 2004; Finlayson et al. 2011), hunting strategies (Estévez 2004; Tortosa et al. 2002), mobility strategies (Burke 2004; Kuhn 1995), competition with carnivores (Churchill 2014; Estévez 2004), division of labor, the presence of trade networks (Horan et al. 2005), and the ways in which hominins modify their environment (contained within Niche Construction Theory, or NCT) (Riel-Salvatore 2010).

As this review shows, different methods of exploring recent hominin niches each provide important perspectives to anthropological research. In order to create results that are theoretically rigorous for both the body of evolutionary theory discussed in Section 2 as well as the previous work discussed in this section, this dissertation uses vocabulary and methods based in ecological research to examine Late Pleistocene hominin population dynamics in Europe. This approach will also allow results from different geographic areas to be rigorously compared to each other. The focus on traditional ecological methods will allows this dissertation to answer anthropological questions concerning the probable distribution of preferred environments of Neandertal and EMHs. In addition, this dissertation expands upon previous research by including samples consisting solely of sites that have produced morphologically diagnostic Neandertal remains. The results of this study are pertinent to investigating the questions raised by the Ebro Frontier Model (EFM) not only in Iberia, but on a continental scale.

4. MATERIALS

The materials used in this dissertation research consist of three paleoenvironmental reconstructions for the time period leading up to Neandertal extinction, plus presence-only location data representative of Neandertal fossil sites, Middle Paleolithic archaeological sites, and Upper Paleolithic archaeological sites. This section discusses the specifics of the paleoenvironmental reconstructions, including which climatic and topographic layers are included, their dating, and their geographic extent. Also discussed here are the presence-data and the rationale for the inclusion of the sites chosen for modeling Neandertal and early modern human (EMH) fundamental niche parameters, and thus the extent of each group's suitable habitat and possible range.

4.1 Paleoenvironmental Reconstructions

Three paleoenvironmental reconstructions were chosen for this project. They cover a continuous 6.8 thousand year period between 43.3 and 36.5 ky cal BP. This time period occurs immediately prior to Neandertal extinction and the proposed last appearance of MP in Iberia at Gorham's Cave, ~26 ky cal BP (Finlayson et al. 2008; Finlayson et al. 2006). They were developed by *Le Laboratoire des Sciences du Climat et de l'Environment* (The Laboratory for Climate and Environmental Sciences) in France and first published by Banks and colleagues (Banks et al. 2008b).

The three reconstructions are centered on Heinrich Event 4. Heinrich Events are rapid onset periods associated with global climatic fluctuations and large-scale melting

of glaciers resulting in massive iceberg sloughing. The massive influx of fresh water from melting icebergs could have interfered with the oceans' circulation patterns, also known as thermohaline circulation (THC) (Heinrich 1988). The cause of these events has not yet been determined (Banks et al. 2008b; Daura et al. 2013; Heinrich 1988). The three reconstructions used here are: Pre-Heinrich Event 4 (Pre-H4) from 43.3 to 40.2 ky cal BP, Heinrich Event 4 (H4) from 40.2 to 38.6 ky cal BP, and Post-Heinrich Event 4 (Post-H4) from 38.6 to 36.5 ky cal BP. The Post-H4 is contemporaneous with Greenland Interstadial 8 (GI8) (Banks et al. 2008b). See Table 1.

Climatic Event	**Temporal Range**
Pre-Heinrich Event 4 (Pre-H4)	43.3 – 40.2 ky cal BP
Heinrich Event 4 (H4)	40.2 – 38.6 ky cal BP
Post-Heinrich Event 4/GI8 (Post-H4)	38.6 – 36.5 ky cal BP

Table 1. The three paleoenvironmental reconstructions used in this study (Banks et al. 2008b).

Eight individual topographic and climatic layers make up each individual reconstruction (Table 2). The layers are commonly used topographic indexes used in GIS analysis. The layers are described here. 1) Accumulation is a compound topographic index which quantifies the tendency for water to pool on the landscape. 2) Aspect measures the angle of the land's orientation to the sun. 3) Elevation is here defined as height above sea level in meters. 4) Slope can be defined as a measure of topographic incline. The environmental variables consist of averaged 5) cold, 6) mean, and 7) warm temperature, as well as 8) mean precipitation. The temperature and precipitation layers in the paleoenvironmental reconstructions were created using common proxies for

examining ancient climates such as Greenland ice core data, Iberian margin cores, and general circulation models (Banks et al. 2006). The LMDZ3.3 Atmospheric General Circulation Model was used specifically for climatic simulations. The topographic variables were generated with the publicly available Hydro-1K dataset created by the United States Geological Survey (USGS). The Pre-H4 encompasses Greenland Interstadials 9 through 11, the H4 reconstructs climate for Heinrich Event 4, and the Post-H4 reconstruction is contemporaneous with Greenland Interstadial 8 (Banks et al. 2008b).

Layer	**Dataset**
Accumulation	Pre-H4, H4, Post-H4
Aspect	Pre-H4, H4, Post-H4
Elevation	Pre-H4, H4, Post-H4
Slope	Pre-H4, H4, Post-H4
Cold Temperature	Pre-H4, H4, Post-H4
Mean Temperature	Pre-H4, H4, Post-H4
Mean Precipitation	Pre-H4, H4, Post-H4
Warm Temperature	Pre-H4, H4, Post-H4

Table 2. Environmental layers included in the paleoenvironmental reconstructions used for this project.

Each paleoenvironmental reconstruction is made up of the same number and type of layers, and contains cells of the same size to create results that are comparable with one another between the three reconstructions. Average values were generated for each cell used in the reconstructions with a resolution of approximately 50 km, or a 0.5 degree/30 arc-minute grid (Banks et al. 2011; Banks et al. 2008a; Banks et al. 2008b; Banks et al. 2008c; Banks et al. 2013a; Banks et al. 2006). A mask layer was employed

to clip all the preceding layers to the extent of the shoreline. Because the sea-level for the three time periods was lower than modern levels, the layers are set at a paleo-shoreline level of -90m. The paleo-shoreline was calculated with current topographic ocean floor data (Banks et al. 2008b).

The study area of this project is contained in a World Geodetic System 1984 (WGS84) georeferenced area between 59.435 and 34.6 degrees latitude and -10.4 and 33.4 degree longitude (Figure 10). This area would normally include a portion of the African continent containing the northernmost sections of modern Morocco, Algeria, Tunisia, Libya, and Egypt. However, because Neandertals have never been documented to occupy these areas during the time period addressed this study, no portions of the African continent were included in the analyses. The climatic variables covering the large bodies of water surrounding the European continent, such as the Mediterranean Sea, Atlantic Ocean, and Black Sea, were also clipped from the study area. Even though there is evidence indicating that late Neandertals and EMHs made use of marine resources (Cortés-Sánchez et al. 2011; Richards and Trinkaus 2009; Stringer et al. 2008), it is unlikely that Neandertals or EMHs would have been able to survive and reproduce on the open ocean for great lengths of time. And, while they did make occasional use of these marine resources this study is interested in modeling their terrestrial habitats. It should be noted that large portions of the Baltic Sea, English Channel, and the present-day southernmost extent of the North Sea are included in the terrestrial areas of the analysis as these geographic regions were exposed at the lower sea levels during the Pre-H4, H4, and Post-H4.

Figure 10. Present-day extent of the paleoenvironmental reconstructions used in this dissertation, including current political boundaries.

The study area consists of 58,251 grid cells and contains many topographic features that could have affected Late Neandertal and EMH movement and the distribution of suitable habitat for each population (Figure 11). These features include mountain ranges such as the Alps, the Pyrenees, the Balkans, the Carpathians, the Apennines, the Pindus, and the Dinaric Alps, as well as high, rugged areas of the Meseta Central on the Iberian Peninsula, the Massif Central located in present-day France, and the Dnieper Uplands in present-day Ukraine. In addition to these mountains and plateaus, lowland areas of the Great Hungarian Plane, the Ebro River Valley, the Po River Valley, the Danube River Valley and corridor, and the Black Sea Lowlands are included.

Figure 11. Physical map of Europe with major topographic features of interest to this study. Modified from a base image courtesy of the National Oceanic and Atmospheric Administration.

Previous research with deep sea cores recovered off the Portuguese coast has been used to conclude that open steppe environments were found to the north and temperate woodlands to the south of the Ebro River Valley until approximately 30 ky cal BP (Zilhão 2009). The topographic and climatological variables used in this study do not include vegetation cover, but levels of precipitation and temperature (which are included) should vary between these two disparate environments. GARP is capable of identifying such differences if they are great enough to make an ecological impact based on the sample of sites used to generate the predictive models.

Other areas of theoretical consideration and experimental design include the risks of projecting niche predictions into the distant past and the grain size of the environmental layers used in the analysis. The environment is not stable and researchers

may not be able to use contemporary environmental data to work with ancient species. If the study focuses many millions of years into the past, modern data detailing landscape attributes such as slope, elevation, drainage index, aspect, and the location of geographic features such as mountain ranges, rivers, and coastlines must be evaluated to determine their appropriateness for use in that particular study. For this project, since the maximum time depth is a fairly recent 43.3 ky cal BP, the use of general topographic variables like elevation, slope, aspect, and accumulation derived from modern data is acceptable. In addition, because the sea-level was lower at that time, a sea-level of 90 meters below current levels was used for the reconstructions (Banks et al. 2008b).

Also, grain size of the environmental layers, or the size of the pixels used in the analysis, needs to be evaluated. Large models in GARP tend to be more sensitive to layers that have different resolution sizes. Having multiple environmental layers with different resolution sizes can negatively affect the predictions (Anderson et al. 2003). All topographic (and climatic) variables in the paleoenvironmental reconstructions used here are scaled to a 0.5 degree/30 arc-minute grid.

4.2 Occurrence Data

This dissertation uses presence-only location data to model the fundamental niche parameters of Late Neandertals and early modern humans (EMHs) in Europe. A site was included in the samples only if it produced materials that have been absolutely dated to one or more of the three paleoenvironmental reconstructions described in the previous section of this section. All dates are reported in calendric years before present

and have, if necessary, been calibrated using the online Cal-Pal tool (Danzeglocke et al. 2015). The occurrence data used in this study were subdivided in several different ways: 1) samples of sites that have produced morphologically diagnostic Neandertal remains, 2) samples of sites with Middle Paleolithic artifacts, 3) a combined sample consisting of both Neandertal remains and Middle Paleolithic sites, and 4) sites with Upper Paleolithic artifacts. A separate sample of locations where morphologically diagnostic EMHs have been discovered during one or more of the paleoenvironmental reconstructions was not created for this dissertation because the sample sizes were too small to produce theoretically rigorous models in GARP. Only one site with non-diagnostic hominin remains with Upper Paleolithic artifacts was identified by this study (Cova Beneito) and was included in the sample of Upper Paleolithic sites.

Certain sites have produced hominin remains that are typically grouped with Neandertals, though they are not truly morphologically diagnostic, in other words these specimens cannot be confidently identified as Neandertal. These remains are typically fragmentary or isolated in nature. However, if these hominin remains were in well-documented association with Middle Paleolithic tools and/or were absolutely dated to one of the three temporal periods used in this study, they were designated as indicative of Neandertals. Each site of this nature was examined on a case by case basis. In this study, only two locations met this criteria for the time period of the Pre-H4 reconstruction: Axlor (Garcia-Diez et al. 2013; González-Urquijo et al. 2014) and Oliveira (Angelucci and Zilhão 2009; Trinkaus et al. 2007; Willman et al. 2012).

GARP requires that all occurrences be spatially unique when calibrating models to within a range of 10 kilometers of each other (Pearson et al. 2007). In order to accommodate this, sites that are located within this narrow geographic window were collapsed into site complexes. For example, Neandertals are hypothesized to have inhabited multiple locations in Gibraltar from prior to the time periods covered by this analysis until the time period that post-dates this study. As these multiple sites are located within 10 km of each other, only one location that produced Neandertal remains (Devil's Tower) was included in the samples in this study. The entire sample of sites with Neandertal remains used in one or more of the paleoenvironmental reconstructions are listed in Table 3.

Site Name	Longitude	Latitude	Country	Included in:
Banyolas	2.77	42.12	Spain	Pre-H4
Zafarraya	-4.13	36.95	Spain	Pre-H4, H4
El Sidrón	-5.33	43.38	Spain	Pre-H4, H4, Post-H4
Devil's Tower	-5.5	36.22	Gibraltar	Pre-H4, H4, Post-H4
Cova Foradá	-0.95	38.9	Spain	Pre-H4, H4, Post-H4
Palomas	-0.895	37.78	Spain	Pre-H4, H4, Post-H4
Feldhofer	6.495	51.228	Germany	Pre-H4
La Quina	0.293	45.51	France	Pre-H4
Les Rochers	0.75	46.415	France	Pre-H4
Le Moustier	1.067	45.00	France	Pre-H4
Mezmaiskaya	32.99	51.72	Russia	Pre-H4
Mezzena	10.99	45.51	Italy	Pre-H4
Axlor *	-2.75	43.14	Spain	Pre-H4
Oliveira *	-8.61	39.51	Portugal	Pre-H4
Lakonis	22.56	36.77	Greece	H4
St. Cesaire	-0.51	45.75	France	Post-H4
Vindija	16.24	46.30	Croatia	Post-H4

Table 3. Sites with diagnostic Neandertal remains included in the project. Sites with an asterisk indicate non-diagnostic remains that were included in the study.

Due to the extremely small number of sites that were available to this dissertation, if the published standard deviation surrounding the date range encompassed more than one temporal period, then the location was included in all time periods pertinent to that reported range. In addition, if a site produced diagnostic Neandertal remains directly dated to one temporal period (for example: the Pre-H4) and Middle Paleolithic tools dated to more than one period (for example: the Pre-H4 and H4), the location was included in multiple temporal periods since the typical interpretation for these types of sites is that this scenario is indicative of extended occupation by Neandertals. While this is perhaps not the most conservative sampling strategy available to the study, it falls in line with conclusions found in the majority of the published literature and allows this study to build slightly larger sample sizes of occurrence data than would be possible otherwise. This strategy for building the samples does most likely produce some statistical noise that can impact the results, but a more conservative strategy would have produced sample sizes so small as to be unusable by the GARP algorithm.

The above strategy impacts the inclusion of sites such as El Sidrón, Devil's Tower, Zafarraya, and Cova Foradá in multiple temporal categories. If the radiocarbon dates reported for the locations were not calibrated, then they were quickly calibrated using the online CalPal tool (Danzeglocke et al. 2015; Weninger et al. 2005) to ensure that all dates used were on the same scale. The numbers reported in the tables are all the calibrated dates. It should also be noted that in a few cases regarding the MP and UP samples, archaeological sites are repeated in both the MP and UP groups for the same

time periods. This is due to a few instances where the MP/UP transition occurs within the temporal boundary of the same time period, such as the sites of El Castillo, Abrigo de Sopeña, and Cova de l'Arbreda. Isturitz was included in this sample by virtue of its archaeological stratigraphy that indicates the site was inhabited from the Early Aurignacian forward through time by early modern humans (EMHs) (Foucher and Normand 2006).

The samples of occurrence points based on archaeological sites were grouped into broadly Middle Paleolithic and Upper Paleolithic categories for analysis. As discussed previously, prior work in paleoarchaeology has focused largely on investigating the possible existence of smaller scale niche differentiation between archaeological populations belonging to either the Middle or Upper Paleolithic (Banks et al. 2011; Banks et al. 2008c; Banks et al. 2013a; Banks et al. 2006; Banks et al. 2013b; Banks et al. 2009). For example, a project might focus solely on constructing predictive niche maps for the Proto-Aurignacian and Aurignacian technocomplexes which are traditionally grouped under the heading of Upper Paleolithic complexes (Banks et al. 2013a; Banks et al. 2013b). For this project, sites belonging to the Middle and Upper Paleolithic were not subdivided into smaller technocomplexes or Cohesive Adaptive Systems (CAS) (Banks 2015; d'Errico and Banks 2013).

Rather than focusing on smaller scale differences between models created for populations of either EMHs or Neandertals, this project sought to investigate large scale differences between Neandertals and EMHs and grouped the archaeological occurrences into categories that best reflect that division. This also speaks to the nature of the method

used for this project. With GARP, separate datasets are required to build and then test the predictive models (Anderson et al. 2003; Pearson et al. 2007; Townsend Peterson et al. 2007). Here the models were built with the larger datasets, the archaeological samples, and tested with the better known, more conservative samples consisting of hominin remains. This allowed the project to build the most robust predictive models possible and then validate those models with locations that we are extremely confident are truly representative of Neandertals or EMHs.

Since this project seeks to examine large scale patterns of Neandertals late-survival/extinction and EMH expansion, the MP and UP archaeological sites were grouped into broad categories, rather than many small ones. Sites were designated as belonging to temporal periods based on absolute dates, if they were available, or accepted time periods for their specific technocomplex. For example, if an archaeological site produced diagnostic Uluzzian tools, but no absolute dates were reported in the literature, it was grouped into the time category dating to ~40,000 – 30,000 years BP, based on the agreement seen in radiocarbon dates from other Uluzzian sites (Riel-Salvatore 2009).

It is very common in anthropological literature to equate Middle Paleolithic industries (including some transitional industries like Châtelperronian, Bohunician, and Uluzzian) with Neandertals (Peresani 2008; Zilhão et al. 2015) and Upper Paleolithic industries (Proto-Aurignacian, Aurignacian, etc.) with EMHs (Banks et al. 2013a; Banks et al. 2013b; Zilhão and d'Errico 1999; Zilhão et al. 2006). In order to give the niche modeling algorithms the best chance of building robust models, this project takes the

less conservative approach of equating Mousterian, Châtelperronian, Bohunician, and Uluzzian sites with Neandertals and Proto-Aurignacian, Aurignacian, Gravettian, Solutrean, Badegoulian, and Magdalenian sites with EHMs. If the results show that the models built with the larger, less conservative archaeological samples fail to predict the sites with morphologically diagnostic Neandertal remains, the author plans in future research to address this question directly and in more detail than is possible for this project.

Even though the primary research question of this project concerns patterns of hominin niches on the Iberian Peninsula, the samples of both archaeological and hominin sites include locations from across Western and Central Europe. If the locations were restricted to Iberia, then the entire model building and analysis would have to be confined to Iberia as well. This would create a situation where the study area was so restricted that the model building and results would suffer. Expanding the samples past the borders of the peninsula increased sample sizes, and allowed the project to have a better chance of building stronger predictive models.

Tables 4 – 12, beginning on the next page, list the Neandertal fossil, MP and UP sites dated to the Pre-H4, H4, and Post-H4. The combined Neandertal fossil and Middle Paleolithic samples are an exact combination of those two samples.

4.2.1 Sample of Neandertal Remains Dated to the Pre-H4

Site Name	Longitude	Latitude	Date	Date Citation
El Sidrón	-4.13	36.95	Occupation from ~35 to 48 ky cal BP	(de la Rasilla et al. 2014; De Torres et al. 2010)
Devil's Tower/Gibraltar Complex	-5.33	43.38	Occupation from ~32 to 47 ky cal BP	(Zilhão and Pettitt 2006)
Zafarraya	-5.5	36.22	39,683 ± 920	(Barroso et al. 2014; Michel et al. 2013)
Cova Foradà	-0.95	38.9	Occupation throughout the MP	(Aparicio Pérez 2014; Aparicio Pérez et al. 2014)
Banyolas	2.77	42.12	~45,000 ± 4,000	(Julià and Bischoff 1991)
Palomas	-0.895	37.78	39,691 ± 926	(Walker et al. 2014; Walker et al. 2008)
Feldhofer	6.495	51.228	40,052 ± 409	(Schmitz et al. 2002)
La Quina	0.293	45.51	Occupation from ~41 to 44 ky cal BP	(Higham et al. 2014)
Les Rochers	0.75	46.415	44,152 ± 817	(Beauval et al. 2006)
Le Moustier	1.067	45.00	Occupation from ~41 to 45 ky cal BP	(Higham et al. 2014)
Mezzena	10.99	45.51	39,724 ± 946	(Condemi et al. 2013)
Mezmaiskaya	32.99	51.72	41,478 ± 399	(Banks et al. 2008b; Golovanova et al. 1999; Skinner et al. 2005)
Axlor	-2.75	43.14	42,100 ± 1,280	(González-Urquijo et al. 2014)
Oliveira	-8.61	39.51	~43,500	(Trinkaus et al. 2007)

Table 4. Sites included in the Pre-H4 (43.3-40.2 ky cal BP) Neandertal sample (*n* = 14).

4.2.2 Sample of Neandertal Remains Dated to the H4

Site Name	Longitude	Latitude	Date	Date Citation
El Sidrón	-4.13	36.95	Occupation from ~35 to 48 ky cal BP	(de la Rasilla et al. 2014; De Torres et al. 2010)
Devil's Tower	-5.33	43.38	Occupation from ~32 to 47 ky cal BP	(Zilhão and Pettitt 2006)
Zafarraya	-5.5	36.22	39,683 ± 920	(Barroso et al. 2014; Michel et al. 2013)
Cova Foradá	-0.95	38.9	Occupation throughout the MP	(Aparicio Pérez 2014; Aparicio Pérez et al. 2014)
Palomas	-0.895	37.78	39,691 ± 926	(Walker et al. 2014; Walker et al. 2008)
Lakonis	22.56	36.77	~40,000	(Harvati et al. 2003; Panagopoulou et al. 2004)

Table 5. Sites included in the H4 (40.2-38.6 ky cal BP) Neandertal sample (*n* = 6).

4.2.3 Sample of Neandertal Remains Dated to the Post-H4

Site Name	Longitude	Latitude	Date	Date Citation
El Sidrón	-4.13	36.95	Occupation from ~35 to 48 ky cal BP	(de la Rasilla et al. 2014; De Torres et al. 2010)
Devil's Tower	-5.33	43.38	Occupation from ~32 to 47 ky cal BP	(Zilhão and Pettitt 2006)
Cova Foradá	-0.95	38.9	Occupation throughout the MP	(Aparicio Pérez 2014; Aparicio Pérez et al. 2014)
St. Cesaire	-0.51	45.75	36,200 ± 750	(Hublin et al. 2012)
Vindija	16.24	46.30	~36,350	(Higham et al. 2006)

Table 6. Sites included in the Post-H4 (38.6-36.5 ky cal BP) Neandertal sample (*n* = 5).

4.2.4 Sample of Middle Paleolithic Sites Dated to the Pre-H4

Site Name	Longitude	Latitude	Date	Dating Source
As Lamas	-7.52	42.55	39,866 ± 3,554	(Zilhao 2006)
La Güelga	-5.11	43.34	42,073 ± 339	(Menéndez et al. 2014)
El Esquilleu	-4.6	43.2	Occupied from ~35 ka to >59 ka	(Baena et al. 2012; Baena Preysler and Carrion Santafé 2014)
El Castillo	-3.97	43.29	~43,000	(de Quiros et al. 2014; Pike-Tay et al. 1999)
Grotte des Fees	3.63	46.39	43,120	(Banks et al. 2008b)
Grotte du Renne	3.75	47.62	42,650	(Banks et al. 2008b)
Combe Saunière	0.16	45.14	42,490	(Banks et al. 2008b)
Grotte XVI	1.2	44.8	42,430	(Banks et al. 2008b)
Roc de Combe	1.35	44.75	41,950	(Banks et al. 2008b)
La Viña	-5.83	43.31	41,043 ± 676	(Santamaria et al. 2014; Wood et al. 2014)
Stranska Skala	13.68	49.82	40,830	(Banks et al. 2008b)
Labeko Koba	-2.49	43.07	40,761 ± 785	(Wood et al. 2014)
Cueva del Mirón	-3.45	43.25	~43,000	(González Morales and Straus 2014)
Abrigo de Sopeña	-4.97	43.34	43,052 ± 741	(Pinto Llona 2014)
Roca dels Bous	0.85	41.87	43,127 ± 900	(Mora et al. 2008; Mora et al. 2014)
Cova Gran	0.81	41.93	~43,000	(Martínez-Moreno et al. 2010)
Las Fuentes de San Cristobal	0.57	42.33	42,998 ± 619	(Ardèvol and Salomó 2014)
Balma dels Pinyons	1.67	41.54	42,397 ± 446	(Vaquero et al. 2013)
Cueva de los Ermitons	-2.59	42.28	40,694 ± 1,774	(Maroto Genover 1993; Maroto 1985)
Cova de l'Arbreda	2.75	42.16	42,813 ±548	(Maroto et al. 2012)
Cueva Millan	-3.45	42.06	42,214 ±520	(Romanillo and Soto 1983)
Sesselfelsgrotte	11.79	48.94	~41,500	(Rots 2009)
Salzgitter	10.327	52.175	~41,500	(Soressi 2005)

Table 7. Middle Paleolithic archaeological sites included in this project dated to the Pre-H4 (43.3 – 40.2 ky cal BP) paleoenvironmental reconstruction (*n* = 23).

4.2.5 Sample of Upper Paleolithic Sites Dated to the Pre-H4

Site Name	Longitude	Latitude	Date	Dating Source
Cueva Morín	-3.82	43.36	41,599 ± 522	(Banks et al. 2013a)
Abrigo de Sopeña	-4.97	43.34	40.3 ± 4.8 ky ESR-LU	(Pinto Llona 2014)
Cova Foradada	-0.12	38.92	39,494 ± 1,012	(Pantoja Pérez et al. 2011)
El Castillo	-3.97	43.29	~41,700	(Banks et al. 2008b)
La Güelga	-5.11	43.34	39,206 ± 1,241	(Menéndez et al. 2014)
Isturitz	-1.2	43.37	41,600	(Banks et al. 2008b)
Grotta de Fumane	10.88	45.55	41,600	(Banks et al. 2008b)
Grotta Paina	11.52	45.43	42,370	(Banks et al. 2008b)
Abric Romaní	1.67	41.54	41,540	(Banks et al. 2008b)
Aurignac	25.42	42.93	~41,000	(Banks et al. 2013a)
Caminade	1.25	44.87	41,320	(Banks et al. 2008b)
Divje Babe I	14.06	46	40,210	(Banks et al. 2008b)
Geissenklösterle	9.78	48.4	41,680	(Banks et al. 2008b)
Hohlenstein Stadel	10.38	48.77	41,860	(Banks et al. 2008b)
Temnata	24.05	43.17	41,140	(Banks et al. 2008b)
Trou al Wesse	5.25	50.47	40,900	(Banks et al. 2008b)
Willendorf	15.4	48.32	42,380	(Banks et al. 2008b)

Table 8. Upper Paleolithic archaeological sites included in this project dated to the Pre-H4 (43.3-40.2 ky cal BP) paleoenvironmental reconstruction (*n* = 17).

4.2.6 Sample of Middle Paleolithic Sites Dated to the H4

Site Name	Longitude	Latitude	Date	Dating Source
As Lamas	-7.52	42.55	39,886 ± 3,554 OSL	(Zilhao 2006)
El Esquilleu	-4.6	43.2	Occupied from ~35 ka to >59 ka	(Baena et al. 2012; Baena Preysler and Carrion Santafé 2014)
Grotte du Renne	3.75	47.62	39,580	(Banks et al. 2008b)
Grotte XVI	1.2	44.8	39,700	(Banks et al. 2008b)
La Viña	-5.83	43.31	40,412 ± 961	(Santamaria et al. 2014; Wood et al. 2014)
Labeko Koba	-2.49	43.07	40,146 ± 554	(Wood et al. 2014)
Abrigo de Sopeña	-4.97	43.34	40,336 ± 975	(Pinto Llona 2014)
Cova de l'Estret de Tragó	0.81	41.93	43,000 ± 4,600	(Casanova et al. 2014)
Lapa dos Furos	-8.41	39.6	38,220 ±724	(Cardoso 2006)
Abric Romaní	1.67	41.54	40,675 ± 978	(Vallverdú et al. 2014)
Cueva Bajondillo	-4.5	36.62	~40,000	(Cortés Sánchez and Simón Vallejo 2014; Maroto et al. 2012)Also Maroto et al. 2012
Cova de l'Arbreda	2.75	42.16	39,160	(Banks et al. 2008b)
Belvis	2.08	42.85	40,110	(Banks et al. 2008b)
Buzdujeni	27.3	48.17	39,910	(Banks et al. 2008b)
Cabezo Gordo	-0.95	37.73	39,690	(Banks et al. 2008b)

Table 9. Sites with MP remains dated to the H4 (40.2-38.6 ky cal BP) paleoenvironmental reconstruction (*n* = 15).

4.2.7 Sample of Upper Paleolithic Sites Dated to the H4

Site Name	Longitude	Latitude	Date	Dating Source
Cueva Morín	-3.82	43.36	40,276 ±1,089	(Banks et al. 2008b)
Abrigo de Sopeña	-4.97	43.34	39,726 ± 891	(Pinto Llona 2014)
Cova de l'Arbreda	2.75	42.17	39,847 ±760	(Wood et al. 2014)
Cueva Bajondillo	-4.59	36.62	38,500 ± 1,789	(Cortés Sánchez and Simón Vallejo 2014)
Cova Foradada	-0.12	38.92	39,494 ± 1,012	(Pantoja Pérez et al. 2011)
Cueva de la Güelga	-5.11	43.34	39,206 ± 1,241	(Menéndez et al. 2014)
Solutré	4.72	46.3	39,440	(Banks et al. 2008b; Banks et al. 2013a)
Abri Pataud	1.01	44.93	39,450	(Banks et al. 2008b)
Combe Saunière 1	0.16	45.14	38,850	(Banks et al. 2008b)
Isturitz	-1.2	43.37	39,830	(Banks et al. 2008b)
Grotta de Fumane	10.88	45.55	39,700	(Banks et al. 2008b)
Paglicci	15.58	41.67	39,180	(Banks et al. 2008b)
Bacho Kiro	25.42	42.93	39,530	(Banks et al. 2008b)
Caminade	1.25	44.87	40,110	(Banks et al. 2008b)
Castanet	1.18	45.03	39,950	(Banks et al. 2008b)
Divje Babe I	14.06	46	40,210	(Banks et al. 2008b)
Geissenklösterle	9.78	48.4	39,660	(Banks et al. 2008b)
Vogelherd	10.07	47.95	38,810	(Banks et al. 2008b)
Wildscheuer	8.17	50.4	39,697	(Terberger and Street 2003)
Hohlenstein Stadel	10.38	48.77	39,420	(Banks et al. 2008b)
Flageolet	0.58	44.82	38,980	(Banks et al. 2008b)
Mochi	7.53	43.78	39,980	(Banks et al. 2008b)
Hohle Fels	9.73	48.37	39,630	(Banks et al. 2008b)
El Castillo	-3.97	43.29	~39,000	(de Quiros et al. 2014; Pike-Tay et al. 1999; Rink et al. 1996)

Table 10. UP sites dated to the H4 (40.2-38.6 ky cal BP) paleoenvironmental reconstruction (*n* = 24).

4.2.8 Sample of Middle Paleolithic Sites Dated to the Post-H4

Site Name	Longitude	Latitude	Date	Dating Source
As Lamas	-7.52	42.55	38,947 ± 3,150 OSL	(Zilhao 2006)
El Esquilleu	-4.6	43.2	Occupied from ~35 ka to >59 ka	(Baena et al. 2012; Baena Preysler and Carrion Santafé 2014)
Lapa dos Furos	-8.41	39.6	38,220 ± 724	(Cardoso 2006)
Cueva de los Ermitons	-2.59	42.28	37,700 cal BP	(Banks et al. 2008b; Maroto Genover 1993)
A Valina	-7.34	43.05	35,519 ± 469	(Banks et al. 2008b)
Almonda	-8.61	39.51	37,100 cal BP	(Banks et al. 2008b)
Jarama	-3.33	40.92	37,560 cal BP	(Banks et al. 2008b)
Labeko Koba	-2.49	43.07	37,800 ± 900	(Wood et al. 2014)
Cova de l'Arbreda	2.75	42.16	37,300 ± 800	(Wood et al. 2014)
Gorham's Cave	-5.35	36.18	37,065 ± 1,1113	(Finlayson et al. 2008)

Table 11. MP sites dated to the Post-H4 (38.6-36.5) paleoenvironmental reconstruction (*n* = 9).

4.2.9 Sample of Upper Paleolithic Sites Dating to the Post-H4

Site Name	Longitude	Latitude	Date	Dating Source
Cueva Morín	-3.82	43.36	38,634-38,015	(Maíllo Fernández et al. 2014; Maroto et al. 2012)
Labeko Koba	-2.49	43.07	38,196 ± 982	(Wood et al. 2014)
Abrigo de Sopeña	-4.97	43.34	37,359 ± 857	(Pinto Llona 2014)
Cova de l'Abreda	2.75	42.16	36,000 ± 700	(Wood et al. 2014)
Cueva Bajondillo	-4.59	36.62	37,500 ± 1,541	(Cortés Sánchez and Simón Vallejo 2014)
Cova Foradada	-0.12	38.92	39,494 ± 1,012	(Pantoja Pérez et al. 2011)
El Castillo	-3.97	43.29	~37,000	(de Quiros et al. 2014; Pike-Tay et al. 1999)
Solutré	4.72	46.3	39,515 ± 990	(Banks et al. 2008b)
Abri Pataud	1.01	44.93	39,497 ± 1,044	(Banks et al. 2008b)
Combe Saunière 1	0.16	45.14	38,977 ± 1,471	(Banks et al. 2008b)
Roc de Combe-Capelle	0.82	44.77	38,368 ± 1,800	(Banks et al. 2008b)
Isturitz	-1.2	43.37	39,810 ± 891 and younger	(Banks et al. 2008b)
Castelcivita	15.23	40.48	36,820	(Banks et al. 2008b)
Grotta de Fumane	10.88	45.55	37,140	(Banks et al. 2008b)
Le Piage	1.39	44.8	37,220	(Banks et al. 2008b)
Bacho Kiro	25.42	42.93	36,660	(Banks et al. 2008b)
Geissenklöstrele	9.78	48.4	37,570	(Banks et al. 2008b)
Lommersum	6.79	50.71	37,152 ± 1,024	(Pastoors and Tafelmaier 2012)
Les Renardières	0.37	45.83	36,520	(Banks et al. 2008b)
Vogelherd	10.07	47.95	37,350	(Banks et al. 2008b)
Hohlenstein Stadel	10.38	48.77	36,700	(Banks et al. 2008b)
Temnata	24.05	43.17	37,670	(Banks et al. 2008b)
Trou Al Wesse	5.25	50.47	36,770	(Banks et al. 2008b)
Flageolet	0.58	44.82	36,530	(Banks et al. 2008b)
Mochi	7.53	43.78	36,720	(Banks et al. 2008b)
Wildscheuer	8.17	50.4	37,070	(Banks et al. 2008b)
Hohle Fels	9.73	48.37	37,350	(Banks et al. 2008b)
Stanska Skala	13.68	49.82	37,420	(Banks et al. 2008b)
Mitoc Malu Galben	27.77	46.38	37,090	(Banks et al. 2008b)
Oblazowa	20.17	49.42	36,830	(Banks et al. 2008b)
Pena de Candamo	-6.08	43.45	36,750	(Banks et al. 2008b)

Table 12. UP sites dated to the Post-H4 (38.6-36.5 ky cal BP) paleoenvironmental reconstruction (*n* = 31).

5. METHODS

The following section includes a detailed discussion of the experimental procedures used in this dissertation to create the consensus prediction maps of the fundamental niche parameters for Neanderthal fossil, MP, and UP samples during the Pre-H4, H4, and Post-H4. It is divided into the different methods used for both small ($n \leq 20$) and large ($n \geq 21$) sample sizes of occurrence data and the specific statistical tests that are most appropriate for each experimental design. In addition, this section addresses the procedures used to process the results and create the consensus prediction maps for each experiment, as well as analyses geared at examining the overlap between the results for different experiments and the geographic density of that overlap.

5.1 The Genetic Algorithm for Rule-Set Prediction (GARP)

The algorithm chosen to produce predictive niche maps for this project was the Genetic Algorithm for Rule-Set Prediction, more commonly known as GARP in the scientific literature. ENM algorithms like GARP were not originally designed to detect the presence of biogeographic frontiers, but it is possible to test for them with these methods. GARP searches for non-random correlates between location data and the environmental variables present at those sites. Areas of complete absence of suitable habitat, might be considered indicative of the presence of a biogeographic barrier. For example, if an ENM analysis predicted a complete absence of environmental variables

associated with the sample sites in the Ebro River Valley, then the hypothesis that it acted as a barrier to Neandertals could not be falsified.

GARP was selected for this study over other algorithms used to make species distribution models (SDMs), such as Maxent, for its ease of use and proven strength when working with small, presence-only datasets (Anderson et al. 2003; Chen and Arratia 2010; Pearson et al. 2007; Peterson and Cohoon 1999; Stockwell 1999; Stockwell and Peterson 2002b). GARP was introduced to the peer-reviewed ecological literature in 1999. The genetic algorithm used by the program was created to work with presence-only data and filter potential error sources in the dataset (Stockwell 1999). The desktop GARP program is freely available for public download at http://www.nhm.ku.edu/desktopgarp/, along with a short procedural manual and Frequently Asked Questions page. This project used the Desktop GARP version 1.1.6.

GARP is a genetic algorithm, classified as an artificial intelligence application, which offers a machine-learning (heuristic) path to predictive modeling that was originally based on research in genetic evolution. It is specifically designed to work with presence-only data (Stockwell 1999). The algorithm produces multiple solutions, or predictive models, when asked to investigate the correlations between species' occurrences and environmental data. These multiple models are then statistically evaluated and summed into one consensus prediction. Potential sources of error can be introduced by omitting sites with relevant data (omission error) and including misclassified sites (commission error) in the sample dataset (Anderson et al. 2003). Algorithms like the Genetic Algorithm for Rule-Set Prediction (GARP) and Maxent

were created in order to deal with research using museum collections and ecological surveys that only documented locations of organism presence (Phillips and Dudík 2008; Stockwell 1999; Townsend Peterson et al. 2007). The focus on presence-only location data is ideally suited to paleoanthropological questions since gaining a true approximation of the absence of fossil species or populations is beyond the scope of the archaeological and fossil record.

5.1.2 Presence-Only Data and GARP

There has been debate in the academic literature concerning the validity of using presence-only samples with algorithms such as GARP. The discussion is germane to this project since it utilized presence-only data. After GARP's debut in the late 1990s, the literature addressed the algorithm's validity and accuracy when modeling animal and plant niches. Stockman and colleagues published a report in 2006 that showed GARP's apparent failures and limitations in spite of its growing popularity in ecological, biological, and anthropological research. Stockman used DesktopGARP to create predictive models of trapdoor spiders in California, USA, by entering forty-two occurrence points from museum and private records into the program to build predictive models of species presence. Stockman's project entered each occurrence point separately and created best-subset predictive models for each of those single occurrence points. The authors found that after 420 best-subset models were created, GARP produced predictions that were neither statistically significant nor accurate (Stockman et al. 2006).

Through discussion of Stockman's methods, a picture was created of how GARP uses location data to generate predictive models and how data is used to enlighten our understanding of a species' fundamental niche parameters. Single location points are not sufficient to generate predictions on the full breadth of any species' fundamental niche. In order to examine the range of environmental variables for which a species is best suited, multiple locations are necessary. Ecological niches are descriptions of the environmental "phenotype" the species prefers (McNyset and Blackburn 2006), or the environment with which the sample of occurrences are associated. While GARP works with a high degree of accuracy for small sample sizes (Stockwell and Peterson 2002a; Stockwell and Peterson 2002b), it still needs multiple points on which to base its predictions. Up to 250 location points may be necessary to reach statistical significance in other predictive modeling programs available to ecologists. However, GARP reaches its maximum accuracy at the inclusion of a set of 100 data points, is near maximum power accuracy at 50 points, and within 90 percent accuracy with only 10 data points (Stockwell and Peterson 2002b). The debate has clarified some of the theoretical and methodological assumptions in using these types of programs, as well as shedding light on which facts researchers need to keep in mind in order to obtain the best, most accurate, and significant results possible (McNyset and Blackburn 2006).

As previously stated, GARP uses presence-only location data to build predictive models. The nature of this technique is ideal for paleoanthropologists and archaeologists seeking to conduct an ENM experiment since accurate absence-data for many paleo-species is difficult or impossible to reconstruct. In order to generate its predictive

models, GARP creates a set of pseudo-absence points, or areas where there are no presence data points entered into the analysis, and combines it with presence points to develop rule-sets to define the ecological niche of the species (Banks et al. 2008c). While the presence-only data that GARP uses works extremely well with paleoanthropological samples, biases can be introduced into the analysis if the fossil or archaeological record is not well resolved. If the record isn't accurate or detailed enough, or not enough sites have been chosen to be included in the study, then GARP will not be able to accurately model the potential distribution of the organisms on the landscape. In addition, not choosing a large enough sample or misidentifying sites, can seriously impact the accuracy of the results (Varela et al. 2011).

Statistically significant results are not always indicative of accurate results. For example, ecological niche predictions were created for the Sasquatch crypto-species, with occurrence data points generated from "sightings" around the United States, which resulted in high statistical significance during model validation (Lozier et al. 2009). This result is not a failing inherent to GARP, but one directly related to the researcher. Erroneous conclusions that appear logical and objective may be easily reached if the researcher is not aware of the constraints and theoretical pitfalls of their study. Essentially, this can be a cautionary tale of garbage in = garbage out. GARP will analyze and create predictive models for whatever occurrence points are plugged into it, regardless of how accurate the sample. This project chose to use a more theoretically conservative sample of only locations that have been absolutely dated to fall within the time periods of the Pre-H4, H4, and Post-H4. While this reduces the total number of

sites available to the analysis, it takes steps to avoid the potential inclusion of incorrectly classified sites.

This study takes explicit steps designed to address these theoretical limitations by carefully evaluating every site included in the various samples used by this dissertation to examine the population dynamics of Late Neandertals and early modern humans (EMHs) in Europe during the Late Pleistocene. As discussed in the previous section, sites were only included in the analysis if they were absolutely dated to one or more of the Pre-H4, H4, or Post-H4 paleoenvironmental reconstructions. Though this procedure reduces the number of sites in each sample, it does reduce the amount of noise that could be introduced to the analysis by the misidentification of sites or including sites that do not actually belong to those time periods.

5.2 Approximation of the Fundamental Ecological Niche

A niche, as defined in the field of ecology, is based on the topographic and climatic variables associated with the physical space an organism occupies on the landscape (Grinnell 1917; Hardesty 1975; Holt 2009; Hutchinson 1957). Ecological niche modelling (ENM) was developed to map the geographic extent of these environmental variables associated with the study organism. ENM has been used to investigate the reconstruction of possible ranges for extinct species, how climate change affects the distribution of modern species, and what paths invasive species may take in the future (Banks et al. 2008a; Banks et al. 2006; Kearney and Porter 2009; Sutton et al. 2007). This dissertation uses methods developed in the field of ecology to investigate the

niche parameters of Late Neandertals and early modern humans in Late Pleistocene Europe. It is tightly linked to the ecological concepts of niches and niche conservatism and how they apply to the study of hominin paleo-populations. This section addresses these concepts and their importance to the experimental design of this project.

5.2.1 The Ecological Concept of the Niche

An ecological niche is generally described as the geographic space on the landscape which contains the environmental variables for which an organism is best suited. Research concerning niches and their expression has been conducted in ecology for a century. Joseph Grinnell, in his work with California Thrashers in the early 20th century (Grinnell 1917), defines a niche as the "sum of habitat requirements that allow a species to produce offspring" (Peterson 2011). In other words, the "Grinnellian niche" concept links a species to its environment where its niche is solely determined by the behavior of the organism and its habitat. The Grinnellian niche concept is behind much of the work in ecology spanning the 20th century and is still considered to be at the heart of ecological research today.

Using Grinnell's work as a base, in the 1950s Hutchinson expanded the definition of a niche to encompass the environmental variables for which an organism displays positive fitness and is best suited, and the expression of those parameters on the landscape (Hardesty 1975; Hardesty 1980; Holt 2009; Hutchinson 1957). Here, positive fitness can be considered to be the relative reproductive success of an organism or population. For the purposes of this project, this would constitute the suite of

topographic and climatic variables which would have allowed Neandertals and EMHs to survive and reproduce and where the pattern of those environmental variables would be on the landscape.

Ecological principles generally hold that niches are distinct between different species in order to reduce the level of competition between them. Species with wider niches, or niches with a wider range of exploited variables, are those that typically deal better with unevenly distributed resources or environmental instability (Hardesty 1975). Wider niches allow organisms to utilize more resources, contributing to their "success." Environmental fluctuations, such as were common in Late Pleistocene Europe, would have more of a deleterious impact on species that could only utilize a narrow range of variables and food sources.

Ecological niche modeling methods (ENM) were developed to examine and quantify the geographic expression of the environmental variables associated with species' presence (Anderson et al. 2002; Anderson et al. 2003; Jiménez-Valverde et al. 2011; Kearney and Porter 2009; Nogués-Bravo 2009; Pearson et al. 2007). Therefore, it is a way to investigate niche parameters and ultimately create maps of the geographic distribution of correlated environmental variables and make predictions regarding an organism's range. These maps are commonly called species distribution maps (SDMs). Many of the initial algorithms developed for ENM required both presence and absence location data of the study organism. However, as discussed in section 5.1.2, acquiring accurate absence data is often extremely difficult, if not impossible, depending on the nature of the subject undergoing investigation (Adjemian et al. 2006; Anderson et al.

2003; Chen and Peterson 1999; Hirzel et al. 2002; McNyset and Blackburn 2006; Pearson et al. 2007; Stockman et al. 2006; Stockwell 1999; Stockwell and Peterson 2002a; Stockwell and Peterson 2002b; Townsend Peterson et al. 2007).

5.2.2 Niche Parameters and the "BAM" Framework

Experiments using traditional ENM methods, such as this dissertation, are constrained by additional theoretical constructs. An organism's ***realized niche*** is defined as its actual geographic distribution. However, ENM does not model the full realized niche of the study species. It only models the geographic range of the environmental variables associated with the presence points introduced to the algorithm by the researcher, otherwise known as the ***fundamental niche***. The fundamental niche of a species defines all the geographic areas where it could *potentially exist*. However, the fundamental niche as described by ENM algorithms may not always match the actual distribution of the species. Other factors besides a single species' or population's habitat preferences also impact the expression of the realized niche. The borders of their range may be constrained by other species competing for the same resources and/or relatively impermeable geographic features, such as oceans, mountain ranges, and large glaciers (Barve et al. 2011; Martínez-Meyer et al. 2004; Peterson 2011; Qiao et al. 2015; Soberón and Peterson 2005).

Three main suites of variables interact to create the realized niche of any organism, including Neandertals and EMHs (Figure 12). First described by Soberón and Peterson (2005), the "BAM" framework describes the interaction of these three factors

and what algorithms like GARP actually model when used to create consensus predictions. The first variable is described as B, or the geographic extent of the space with favorable biotic variables for organism survival and reproduction, such as food resources. The second is A, or the geographic extent of the space with favorable abiotic (environmental) variables for presence, also known as the fundamental niche parameters. These typically include climatic and topographic variables in environmental reconstructions. The last factor is M, or the geographic space that is accessible to the organism on the landscape (i.e. the species' movement across the landscape) (Peterson 2011; Soberón and Peterson 2005).

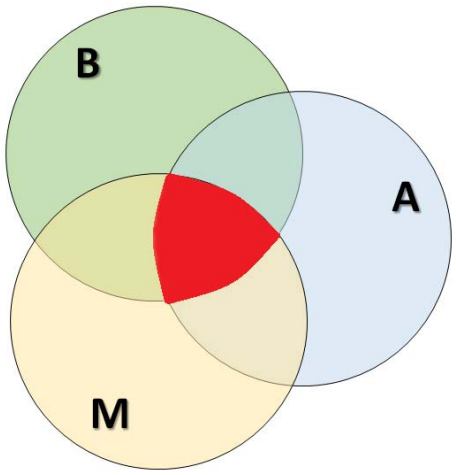

Figure 12. The BAM framework for describing factors affecting the geographic extent of the realized niche (adapted from Soberón & Peterson 2005:3).

Algorithms commonly used to create species prediction maps, such as GARP and Maxent, model A from the BAM framework. In other words, these predictive models

only map the extent of the fundamental niche parameters associated with the locations (species presence points) provided to the algorithm (Soberón and Peterson 2005). These abiotic variables can include both topographic and climatic factors such as elevation, slope, precipitation, and temperature. The results of this project consist of a suite of maps displaying the geographic extent of these variables found in association with Neandertals, MP sites, and UP sites. Analysis of the overlap between these predictions was also conducted.

The researcher can manually take M into account by restricting the study area to the geographic extent in which they know the organism has historically existed. M can include impermeable topographic features, such as large mountain ranges and bodies of water. If areas outside of the organism's M are included in the study area, the algorithm will attempt to predict presence/absence in those areas. Also, if similar abiotic variables associated with species locations are found in areas outside the true M, then the algorithm has a high likelihood of predicting those areas as present. Both of these situations could skew the validation toward a less statistically significant result than one would obtain with a more accurate reflection of M. A real world reflection of M is not always obtainable, especially if the study organism is an extinct species or if the researcher is projecting the niche between time periods to the distant past. The researcher's approximation of M is a hypothesis, especially when studying fossil species.

For this study, a true approximation of M is unattainable because the paleo-populations consisting of Neandertals and EMHs are no longer present. Thus, M must be reconstructed using previously published research in anthropology regarding what we

know about the behavior and ecology of Neandertals and EMHs. For the purposes of this project, large bodied hominins would have relatively few geographic restrictions to their movement across the landscape. Oceans and ice sheets during glacial conditions would be some of the only major topographic factors limiting their movement. Both these were taken into account in the paleoenvironmental reconstructions. Oceans were completely cut from the study area by using a mask layer to restrict the algorithm to modeling only terrestrial areas. The extent of the ice sheets was also modeled in the Pre-H4, H4, and Post-H4 by the original authors and was set up as boundary in the reconstructions (Banks et al. 2008b).

The suite of variables that make up the factor B are very difficult to reconstruct for extinct species. B includes the geographic area with the presence of other biotic organisms that are *favorable* to the study organism's survival and reproduction (Soberón and Peterson 2005), such as food sources and the absence of competing organisms (Barve et al. 2011; Peterson 2011; Soberón and Peterson 2005). For large bodied hominins like Neandertals, B could cover a large range of faunal and floral species. Faunal remains from Neandertal and MP sites have shown reliance on large bodied herbivores, such as steppe bison, red deer, horse, ibex, caribou, goat, Saiga antelopes, and wild ass. For many years it was thought that Neandertals ate almost no plant resources and made no use of avian and aquatic resources across the entirety of their temporal and geographic range. This assumption was based on the faunal remains typically found at MP sites and isotopic analysis of a few Neandertal remains (Hoffecker 2009). However, the validity of the isotopic studies has been called into question on both

the basis of their biological meaningfulness as well as the fact that the only Neandertals sampled thus far have been from non-coastal environments (Hardy 2010; Hardy and Moncel 2011).

Archaeological data has also found evidence of seasonal use of MP sites in Europe where Neandertals were actively pursuing large bodied herbivores (Hoffecker and Cleghorn 2000). In addition, the study of late surviving Neandertal sites in Spain has indicated that Neandertals were eating avian and aquatic resources (Stringer et al. 2008). Analysis of Neandertal dental calculus from remains found at Shanidar and Spy include floral microfossils of grasses, legumes, and date palms (Henry et al. 2011). It is therefore apparent that the understanding of Neandertal diets across time and space is still evolving. The sheer number of biotic variables with which Neandertals interacted makes it very difficult to reconstruct a continent-wide depiction of anything but the most basic of pictures. Consequently, the modeling of B is currently beyond the scope of algorithms such as GARP.

Ultimately, species distribution models (SDMs) such as the ones created in this study are hypotheses about the geographic extent of the fundamental niche for Late Neandertals and early modern humans (EMHs). There are theoretical limitations on how far we can push the ability of these algorithms to model meaningful suitable habitats or species' ranges. However, ecological niche modeling (ENM) methods take specific steps that are designed to counteract or see past the problems introduced by using presence-only data from the fossil and archaeological data and our inability to fully reconstruct species' absence.

5.2.3 Niche Conservatism

Niche conservatism is the theory that fundamental niche parameters will remain stable for extended time periods and will only change or evolve slowly (Peterson and Martínez-Meyer 2007), allowing researchers to use predictive modeling programs to project the ranges of a species' niche to the future or distant past. This concept is the basis of how algorithms like GARP are able to predict, to a high degree of accuracy, the presence and absence of species on the landscape and the path an invasive species will take. For example, the possible path invasive species might take when introduced into a new geographic area can be predicted only if the invasive species' niche does not dramatically change when entering a new geographic area (Peterson and Vieglais 2001).

Some research calls into question the validity of niche conservatism with regards to Pleistocene species, stating instead that a species' distribution can change and shift when coming into contact with other potentially competitive species (Martínez-Meyer et al. 2004). It is generally thought in ecological research that high levels of niche conservatism for faunal species is the norm rather than the exception. Over the last fifteen years, efforts have been made to quantify and explicitly test assumptions regarding niche conservatism. These studies have found that niches tend to be conserved, or show little to no modification in their environmental association, on the span of tens to tens of thousands of years (Chen and Peterson 1999; Peterson 2011; Peterson and Nyari 2008).

Quantifying niche conservatism is particularly important for studies that project niche parameters from one time period to another, either into the future or into the

distant past, in order to examine the change in geographic area over time. Assumptions of niche conservatism are made when modeling the distribution of past populations of organisms using their contemporary descendants. Previous studies have projected ranges with high degrees of statistical accuracy and significance (Banks et al. 2008a; Chen and Arratia 2010; Waltari and Guralnick 2009).

Preferably, levels of niche conservatism can be examined or addressed when building a study, but it is somewhat unsafe to assume a species has a long history of niche conservatism when projecting between time periods. This study does not project between time periods. Instead, niche "snapshots" were built for the three paleoenvironmental reconstructions chosen using contemporaneous locations of Middle Paleolithic archaeological sites and Neandertal hominin remains. This reduces the impact that an unstable niche, one that is either contracting or expanding, could have on the results.

It should be noted that true niche expansion or contraction is not necessarily expressed in the geographic fluctuation of the environmental variables correlated with species presence. Niche parameter expansion would be illustrated in a situation where an organism begins to utilize previously unused environmental variables. Conversely, niche parameter contraction could only truly occur when an organism stops using previously included environmental variables. For example, if an organism was previously able to make use of landscape at an elevation range of 250 to 500 meters, but, after a certain point was able to inhabit areas between 0 to 1,000 meters in elevation, the conclusion could be drawn that organism's niche parameters had expanded. Thus, unless a similar

situation is observed in the fossil and archaeological data, it cannot be concluded that the EMH niche had "expanded" nor the Neandertal niche "contracted." Tests of niche identity have been developed to quantify this situation and will be used in future analyses to examine Late Neandertals and EMHs (Peterson 2011).

5.2.4 The Principle of Competitive Exclusion

Competitive exclusion is another underlying principle of studies utilizing ENM methods. It states that two species cannot exist in the same ecological niche without one going extinct or being forced out of that niche. For example, with Neandertals and EMH, competitive exclusion is the basis of the assumption that these two closely related hominin populations could not have existed in the same niche without one going extinct. The competitive exclusion principle is one commonly used in ecology and biology and was generated from the work of Lotka and Volterra completed in the 1920s. The principle states that there are four possible scenarios that may occur when two competing species meet and attempt to occupy the same niche at the same time, if the resources are sufficient enough to allow either the hypothetical Species 1 or Species 2 to survive (Godsoe and Harmon 2012).

As shown in Table 13, there are four basic scenarios that ecologists have outlined based on the competitive exclusion principle for when competing species meet on the landscape. The first is that Species 1 will out-compete Species 2 and Species 2 goes extinct or is forced out of the niche. The second is the reverse of the first scenario. The third scenario results in periods of equilibrium if the resources are abundant enough, but

one species will still eventually out-compete the other. The fourth scenario requires abundant natural resources for a period of equilibrium between the two species, but eventually the two groups will undergo a process of niche differentiation, also known as niche partitioning, in order to prevent contact and competition between multiple groups occupying the same niche. True equilibrium with no niche partitioning is rare in the natural world and requires abundant resources. It is typically seen when species use different techniques to access the resources or accesses them at different times from each other, as is seen in some bird species (Hardesty 1975).

	Species 1	**Species 2**
1	Survives	Extinction
2	Extinction	Survives
3a	Equilibrium with eventual survival	Equilibrium with eventual extinction
3b	Equilibrium with eventual extinction	Equilibrium with eventual survival
4a	Equilibrium with eventual niche partitioning	Equilibrium with eventual niche partitioning
4b	Long-term equilibrium with no niche partitioning	Long-term equilibrium with no niche partitioning

Table 13. Scenarios and outcomes involving the principle of competitive exclusion (adapted from Hardesty 1975).

Thus, when anthropologists hypothesize that Neandertals went extinct due to competition with modern humans (Banks et al. 2008b; Banks et al. 2013b), they are drawing heavily on the assumptions that: A) Neandertals and modern humans had overlapping or extremely similar niches, and B) that two similar species cannot occupy the same niche on the landscape at the same time. Additionally, hypotheses of Neandertal extinction based on changing climate are rooted in the ecological principle of

niche conservatism and assuming their niche could not adapt to or tolerate the environmental fluctuations.

5.3 Experimental Design with GARP

Experiments run with ENM algorithms like GARP are initially designed with later statistical validation procedures in mind. These are geared toward the organization and retention of known test points, which are taken out of the initial sample of sites chosen for the experiment. It is theoretically unsound to test the predictive models generated by GARP with the points used to build those models (Pearson et al. 2007), so the points used to validate models are removed from the initial sample and reserved for later validation practices. Using the same presence points to generate and validate the consensus prediction would skew the results and produce models that were erroneously more highly significant. In other words, building and testing a model with the same points, it will automatically predict those points as present. Since the types of statistical tests used to validate models vary with the sample size, those samples are organized in different ways to reserve the number and type of test points required for the different tests chosen by the researcher.

For this study, the statistical validation methods used for sample sizes of 20 or fewer differ from larger sample sizes of 21 or more presence points. Consensus models generated from small samples were later validated with Pearson's P-Value Compute (Pearson et al. 2007) while consensus models from larger sample sizes were validated with cumulative binomial probabilities and Partial-ROC tests (Peterson et al. 2008).

These different statistical tests require different data from the results in order to properly run the validation analysis. In order to produce the proper data that these statistical test need, the experimental design differed between small and larger sample sizes. This experimental design controls the procedural steps taken even before the first experiment is run in Desktop GARP. Experimental design for small sample sizes are discussed in Section 5.3.1 while the design of larger sample sizes is covered in Section 5.3.2.

The last type of experiment generated for this dissertation consisted of consensus models created using samples of Middle Paleolithic archaeological sites at which morphologically diagnostic hominin remains have never been discovered. The test points used to validate this type of experiment consisted of the sites with Neandertal fossil remains dating to the same paleoenvironmental reconstruction. Cumulative binomial probabilities and Partial-ROC tests were also chosen for the statistical validation of these experiments. The specifics of this experimental design are discussed in Section 5.3.3.

5.3.1 Small Sample Design

There are special techniques for formatting the location data of extremely small samples, classified for this dissertation as those samples of 20 or fewer presence points. These require specific formatting in Excel 2013 in order for correct processing with statistical packages such as Pearson's P-Value Compute. This formatting is quite different from the formatting required for slightly larger datasets that will be statistically tested with cumulative binomial probabilities or partial-ROC analyses. Pearson's P-Value Compute requires that the sample of presence points be organized in a modified

jackknife *n – 1* format (Pearson et al. 2007), where the sample is repeated equal to the total number of the sample and a different point is omitted from each repeat. Each *n – 1* repeat of the sample is run through GARP with the standard best-subsets procedures discussed in Section 5.4. This *n – 1* technique maximizes the size of the training set of points used to build the predictive model and still allows for adequate testing later (Pearson et al. 2007). The specifics of the Pearson's P-Value Compute validation process are discussed in Section 5.5.2.

5.3.2 Large Sample Design

The statistical tests used in the validation procedures for samples of 21 or more presence-points are cumulative binomial probabilities and Partial-ROC. Critical binomial values were also examined for consensus models generated with larger sample sizes, though this test is not a true part of the statistical validation procedures. Cumulative binomial probabilities and Partial-ROC tests require that the experiment be designed in a manner different than was described in Section 5.3.1 for small sample sizes. These tests require multiple test points, rather than the single points of the previous *n – 1* structure. In order to gather multiple known test points, each large sample was sorted randomly and split into separate training (the points used to generate the predictive model in GARP) and test set (those points omitted from the GARP analysis and reserved for later statistical validation) (Pearson et al. 2002; Pearson et al. 2007). This randomization and splitting/sorting was repeated five times during the experimental design in order to ensure rigorous statistical validation later in the procedure. The

specifics of the cumulative binomial probabilities and Partial-ROC test are covered in Section 5.5.3.

5.3.3 Samples of Middle Paleolithic Sites Tested with Neandertal Fossil Locations

In addition to the standard procedures for samples described in sections 5.3.1 and 5.3.2, the researcher may also choose to generate a predictive model with one sample and test it with another. This is only an appropriate method under certain circumstances. The two samples must not have any overlapping occurrences, as it is pointless to attempt to test a model with the locations used to build it (Pearson et al. 2007). Doing so will only skew the results as those points will already be predicted as present by all experimental runs generated by GARP. The sample of occurrences used to test the models must also be appropriate to the experiment's design. If the model is built with a sample of occurrences dating to the period of H4, and no projection to another time period is built into the experimental parameters, then the sample used to test that predictive model must also date to the H4 period. For example, an appropriate experiment under these conditions could have a model calibrated with locations of Middle Paleolithic archaeological sites and then be tested with the locations of morphologically diagnostic Neandertals. In this case, the $n - 1$ or random split and sort procedures are not needed, as the sample of archaeological sites acts as the training set and the sample of Neandertal fossil remains acts as the test set for these models.

This type of experiment allowed this dissertation to begin to address questions concerning the ability of predictive models created with archaeological sites to

accurately predict locations of Neandertal fossil remains. In other words, it investigates questions concerning the appropriateness of using archaeological data to stand as a proxy for a biological population during the Late Pleistocene in Europe. This debate on technocomplexes versus populations was discussed in detail in Section 3.1.1 of this document.

5.4 Dealing with Model Variation – Standard Best Subsets Procedures

Standard GARP best-subsets procedures were used for this project as were described by Anderson, Lew, and Peterson (2003). These procedures are very beneficial to the ultimate generation of consensus prediction maps as they enable the researcher to control for model variation. Standard procedures for this project required GARP to create 200 runs during a single experiment with a maximum of 1,000 iterations in the optimization parameters. GARP will generate up to 200 separate predictive models per experiment. As utilized here, GARP will run up to a maximum of 1,000 iterations, or until the algorithm reaches the point of convergence, where the addition of new rules available to the program (atomic, range, negated range, and logistic regression) have a negligible effect on the program's intrinsic accuracy measures (Anderson et al. 2003). This creates the occasional situation where GARP will be asked to create 200 models, but will reach convergence after a smaller number. Best-subsets procedures, however, will always automatically choose the 10 best models out of however many the algorithm generates for that particular experiment.

As discussed in Section 5.3.1, a small sample where *n* is less than or equal to 20 locations is organized in a modified jackknife *n – 1* manner. Each *n – 1* set of points is separately run through GARP and asked to generate 200 predictive models for each set of points. The best-subsets procedures then automatically choses the 10 best out of each of those 200 models for all of the *n – 1* sets. The 10 best models for each set is then taken to other programs for statistical validation and the creation of the consensus prediction maps. Thus, the number of times that GARP is run in order to generate the consensus prediction is equal to the sample size.

If best-subsets procedures were not employed, the amount of data that GARP would generate would be very difficult to process and refine into the single set of consensus prediction maps that are the main goal of this process. For example, if a sample of 17 points, organized in *n – 1* fashion, was fed into GARP without using best-subsets procedures, up to 200 models would be generated for each of those sets resulting in 3,400 separate predictive models that the researcher would then be required to process.

Using best-subsets for the same example would only result in a maximum of 170 models, 10 for each of the 17 *n – 1* runs, for later processing and validation. The randomization and splitting/sorting procedures for sample design described in Section 5.3.2, mean that larger samples (those equal to or greater than 21 presence points) are only run through Desktop GARP 5 times rather than a number equal to the sample size (as with the *n – 1* design for smaller sample sizes). Here GARP generates up to 200 models for each of the 5 runs and, with best-subsets procedures, only the 10 best of those

are retained, resulting in a total of 50 models for later processing, validation, and the creation of the consensus prediction maps.

5.5 Validation of the Consensus Models

Validation analyses of the predictive models created by ENM methods are an important part of the research design. It is through the completion and interpretation of these statistical tests that the researcher can determine whether or not the consensus prediction models generated by algorithms such as GARP create models that make a meaningful contribution to the body of knowledge. Statistical validation used in this dissertation seeks to determine whether or not the consensus prediction models can correctly classify known test points at a better than random rate. In other words, these tests examine whether the model correctly classifies the known omitted points in the group being modeled (in this case, Late Neandertals or EMHs), i.e., does it show that the known point was actually present at that particular present at that particular time? The probability values (commonly known as *p*-values) indicate how likely the results are to have occurred if the data was random. Here the testing procedures were organized around a standard null versus alternative hypothesis where *p*-values of 0.05 or less indicate that the null hypothesis of randomness can be rejected, or, that these results are not likely to have occurred at random.

As was discussed in Section 5.3, Pearson's P-Value Compute was used with small sample design and cumulative binomial probabilities and Partial-ROC were used with large sample design. The types of statistical tests appropriate for model validation

are restricted by the nature of the data itself. Since presence-only data is used here, indices like kappa and the standard area under the receiver operating characteristic curve (AUC curve) are not appropriate (Pearson et al. 2007). There is some overlap in sample sizes where the choice between using Pearson's p-value and cumulative binomial probabilities/partial-ROC must be made (Pearson et al. 2007; Peterson et al. 2008). For consistency in this project, all samples under an n of 20 were tested with Pearson's p-value and all those with an n of 21 or greater were tested with cumulative binomial probabilities and partial-ROC. The following discussion of validation procedures are divided between small samples ($n \leq 20$) and larger sample sizes ($n \geq 21$). The specific procedural steps for the different methods of statistical evaluation of the predictive models in this project will be detailed in Sections 5.5.2 and 5.5.3.

5.5.1 Thresholding

The validation procedures of Pearson's P-Value Compute and cumulative binomial probabilities require that test points be classified by the predictive models as either present or absent. The known test points are viewed as trials and a classification for a known test point of present constitutes a successful trial by the predictive model generated by GARP while a prediction of absent for a known test point constitutes an unsuccessful trial. To gain this information on which test points are predicted present or absent, a decision must be made on which pixels in the model can be classified present or absent. This process is commonly known as thresholding (Pearson et al. 2004; Pearson et al. 2007) and also describes how many of the models used to build the

consensus prediction model are in agreement on whether or not that test point is predicted as present. Thresholding procedures were carried out for predictive models created with both small and large sample sizes.

Standard lowest presence threshold (LPT) practices as described by Pearson and colleagues (2007) were used in this study where the threshold was set at the number of models in agreement for a test point. As Pearson and co-authors state, "This approach can be interpreted ecologically as identifying pixels predicted as being at least as suitable as those where a species presence has been recorded…" (2007:107). In other words, for this study, these thresholded consensus predictions identify habitats for Late Neandertals and EMHs that are at least as suitable as those found in their absolutely dated, known locations during the Pre-H4, H4, and Post-H4. Or, that those pixels classed as present in the consensus predictions mark the location where habitat was identified that was as suitable as that found where Neandertals and EMHs were known to be in the archaeological and fossil record.

The only statistical test used in this dissertation that does not rely on thresholded information is the Partial-ROC test and, as such, does not require decisions to be made by the researcher regarding what constitutes presence and absence. The Partial-ROC test is beneficial for validation purposes alongside thresholded tests as it examines the full spectrum of data generated by the best-subsets models, rather than reducing the entire best-subset run to one map of presence versus absence. This test is also a good compliment to the more traditional cumulative binomial probabilities as it weights omission error, where points we know are present are incorrectly classified as absent,

much more heavily than commission error, where areas that are actually unsuitable are included in the model (Peterson et al. 2008).

5.5.2 Validation of Models Created with Small Sample Sizes

Pearson and colleagues (2007) developed a statistical test and technique for small sample sizes used with the GARP algorithm. The statistic is based on a jackknife technique where GARP is used to generate models of successive sets of $n - 1$ occurrences, with a different location left out each time. In the following formula, P_i is the ratio of area predicted present after deletion of the ith occurrence, X_i is the success-failure measure indicating if the ith point is predicted present or absent (where predicted present has a value of 1 and predicted absent has a value of 0). H is the assumption of random assignment where X_i is a random trial with probability of success indicated again by P_i. In the formula, successes (times the ith occurrence is predicted present) are weighed more than the failures (times the ith occurrence is predicted absent) and the resulting p-values have been found to be accurate when examined and compared with other methods. The test examines whether or not the summed models predict the ith point at a better than random rate (Pearson et al. 2007).

$$D = \sum X_i(1 - P_i)$$

The formula assumes independence of the jackknife trials, even though it should be noted that the trials are not strictly independent as they do share the locations of the

non-omitted points. The procedure ensures that presence/absence values and ratios of pixels in the study area predicted present divided by the total number of pixels are generated for each omitted (*i*th) location. While not independent in the strictest sense of the word, repeated use and testing has demonstrated that the *p*-values produced by this formula are, "…at least approximately correct, and therefore provides a useful measure of predictive ability" especially for samples where $n < 25$ (Pearson et al. 2007).

In other words, each test point from an $n - 1$ best-subsets experimental run results in a value of 1 (a successful trial where the test point is correctly classified as present) or 0 (an unsuccessful trial where the known test point is incorrectly classified as absent). These successful or unsuccessful trials for each omitted test point are then combined with the proportion of pixels predicted present to the total number of pixels in the study area in each omitted test point's particular $n - 1$ run. This allows the formula to evaluate the multiple jackknifed runs with a sliding probability scale and result in a single *p*-value.

5.5.3 Validation of Models Created with Large Sample Sizes

Two statistical validation methods were chosen for larger samples sizes in this project: 1) cumulative binomial probabilities and 2) Partial-ROC curves. A cut-off point of $n \geq 21$ was established for all experiments in this dissertation project where those experiments with samples below that bar were treated with the above Pearson's *p*-value, while those at or above that cut-off were treated with cumulative binomial probabilities, critical binomial values, and partial-ROC analysis. Larger and more complicated

statistical tests were not utilized here since these samples are still very small when compared to typical sample sizes found in current ecological research. Thus, one-tailed binomial probabilities and modified partial-ROC analyses are more appropriate than χ^2 or area under the receiver operating characteristic curve (also known as AUC or AUROC) (Anderson et al. 2003; Pearson et al. 2007; Peterson and Martínez-Meyer 2007; Peterson and Nyari 2008).

As discussed in Section 5.3.2, covering the experimental design of the larger sample sizes in this study, these consensus prediction models were generated by repeating the randomization and splitting/sorting process 5 times. Cumulative binomial probabilities, critical binomial values, and Partial-ROCs were calculated for each of those repetitions. This results in 5 different values for each of those tests, rather than the single *p*-value generated by Pearson's P-Value Compute. Each of the values is reported in the results section, but the consensus predictions can be described as having *p*-values less than or equal to the highest value generated by each test.

5.5.3.1 Cumulative binomial probabilities & critical binomial values

One major benefit of using cumulative binomial probabilities is that they require no special programs to calculate and can be run in any version of Microsoft Excel. In the following formula, π equals the probability of success of one trial. *S* equals the number successful trials or the number of test points predicted present. *N* is equal to the total number of trials or total number of test points used to validate the model. *P* stands for the proportion of pixels in the study area predicted present divided by the total number

of pixels in the study area. And α stands for the acceptable error level, also sometimes called the significance level. The test will result in a decimal less than 1.0 which, if greater than 1.0 minus the acceptable α-level, indicates the model predicted test occurrences at a better than random rate. Typical α-levels in most published literature are set at 0.05, thus if the cumulative binomial probability results in a decimal greater than or equal to 0.95 the model is concluded to predict the test points at a greater than random rate. In order to present the result of cumulative binomial probabilities in a manner similar to how *p*-values are reported in peer reviewed literature, where the resulting number is significant if a result of 0.05 or less is generated (equal or less than the chosen α-level), the formula only changes to 1 minus the number given by the cumulative binomial probability formula.

$$\pi = (S,N,P)$$

In order to complete the cumulative binomial probability in Microsoft Excel, the formulas are reported below. The first is for the standard reporting of a significant result if greater than 0.95 (1.0 minus the α-level of 0.05). The second is for a result more similar to the standard method of reporting *p*-levels, with a significant result if less than 0.05 (with the accepted α-level set at 0.05). All probability values using this test in the results of this dissertation are reported using the second formula.

=BINOM.DIST(*S*,*N*,*P*,TRUE)

=1-BINOM.DIST(*S*,*N*,*P*,TRUE)

Another easily run test with Microsoft Excel employed for larger samples sizes in this project is the critical binomial value. It generates the number of successful trials needed for that predictive model to be classified as statistically significant when running the cumulative binomial probability. In other words, the critical binomial value is the value at which the model passes the tipping point and is able to classify test points at a better than random rate. While it is not a test used to validate the quality of the consensus predictions, it is an interesting complimentary form of data analysis that allows for the examination of how close or far the models generated are from that proverbial tipping point. The formula needed for use in Microsoft Excel is listed below.

=CRITBINOM(*N*,*P*,*A*)

N stands for the number of trials in the experiment, or the total sample size of the test points. *P* stands for the proportion of pixels in the study area predicted present divided by the total number of pixels in the study area. *A* equals $1 - \alpha$ and stands for the confidence level at which the acceptable error limit is set, i.e. at what decimal point the researcher accepts that the test will predict test points as present in a greater than random rate.

5.5.3.2 Partial-ROC testing

The modified partial-ROC test was created to take into account concerns that standard ROC-AUC (also known as AUROC) tests were not theoretically appropriate for the nature of smaller, presence-only datasets (Anderson et al. 2003; Pearson et al. 2007; Peterson et al. 2008). The main reason for this theoretical incompatibility is that with traditional receiver operating curves, omission error (omitting sites with relevant data) and commission error (including misclassified sites) are weighed the same. However, researchers conducting ecological niche modeling analyses care far more about omission error than commission error. A traditional AUROC also "systematically undervalues models that do not provide predictions across the entire spectrum of proportional areas in the study" (Peterson et al. 2008)

The modified partial-ROC test proposed by Peterson and colleagues in 2008 takes this into consideration. This test takes into account the full range of successful trials, including those where only some of the best-subset models predict the points as present, whereas cumulative binomial probabilities only register a success as one where all 10 best-subset models predict the point as present (Peterson et al. 2008). The modified partial-ROC test is publicly available at the website http://shiny.conabio.gob.mx:3838/nichetoolb2/ under the SDM performance dropdown menu and only requires the exported ASCII file of the summed predictive model and the occurrences file (presence data) in CSV format.

The Partial-ROC parameters used here sets the proportion of omission (acceptable error) at 0.05, the random points percentage at 50, and the number of

iterations for the bootstrap at 1,000. When the output table is produced, it is easily downloadable to Microsoft Excel. For a significant test, there should be many numbers in the AUC_ratio column that are equal to or greater than 1.0. The other columns produced by the test are not of interest for this analysis. After the table is imported into Microsoft Excel the function =COUNTIF(D2:D1001,"<=1") gathers the total number of iterations less than or equal to 1. Since the proportion of omission is set at 0.05, this means that the AUC_ratio column must have 50 or less times (as 50 is 5% of 1,000 iterations of the bootstrap) when the number drops below 1.0 before the test became non-significant. For example, if the "countif" function in Excel produced a number of 37, this indicated a *p*-value of 0.037 with 1,000 runs and thus a significant result where the null hypothesis that the results being tests resulted from random chance was rejected.

5.5.4 Validation of Models Created with Middle Paleolithic Sites and Tested with Neandertal Fossil Locations

Predictive models created with Middle Paleolithic archaeological sites and validated with Neandertal fossil locations were also included in this study, as described in section 5.3.3. Since the training and test sets were created from discrete samples of non-overlapping locations, test sets consisted of multiple points and thus it was necessary to use cumulative binomial probabilities and Partial-ROC tests for statistical validation. However, in contrast to the validation procedures described in the previous section, these tests are only performed once as there was no need for the randomization

and splitting/sorting procedures. This results in a single value for each statistical test rather than multiple values.

5.6 Post-Processing of Consensus Prediction Models

One of the goals during the processing of the consensus prediction models is to create a single map or a small set of maps that illustrates the geographic extent of the areas predicted present and absent by those models. These typically take the form of bicolor presence/absence maps or a heat map with more than two colors. Majority, minimum, and maximum consensus prediction maps were generated in the results of this dissertation for small and large sample experiments. A single thresholded presence/absence map and one map of the unthresholded results for the predictive models created with Middle Paleolithic archaeological sites, but tested with Neandertal fossil locations (as described in Section 5.3.3 and 5.5.4). In addition to the consensus prediction maps described above, an analysis of the overlap between the combined Neandertal/Middle Paleolithic sample and the Upper Paleolithic experiments for the Pre-H4, H4, and Post-H4 was conducted to determine the exact geographic overlap of areas predicted as present by both models.

5.6.1 Creating the Consensus Prediction Maps

Four maps illustrating the consensus prediction models were created for the small and large sample size procedures in ArcGIS 10.2: majority, minimum, and maximum. The majority map classifies pixels as present or absent based on what they were

classified as the majority of the time based on all the models used to create the consensus prediction. In other words, pixels are predicted as present if they were previously predicted present at a rate of 0.5 or greater. The minimum map classifies pixels classified as present only if all models predict them as present. This is the most conservative final map of the consensus prediction that can be generated. The maximum map shows pixels classified as present if any of the models ever classified them as present. This is the least conservative map that can be generated.

5.6.2 Overlap Analysis

An overlap analysis was conducted on the majority consensus prediction maps to compare the Neandertal/Middle Paleolithic and Upper Paleolithic results for the Pre-H4, H4, and Post-H4. The majority predictions were used instead of the maximum and minimum as they offer a compromise between the most and least conservative predictions generated by the previous experiments. The overlap maps generated for this dissertation illustrate the exact geographic area where each of the models illustrating Late Neandertal and EMH suitable habitat are predicted as present. In other words, this exploratory analysis identifies areas where the suitable habitat for these two groups overlapped and offers insight into exactly where it is very likely these two groups came into contact with one another.

6. RESULTS

This section will address the results of the following experiments that produced consensus predictive models of fundamental niche parameters for the Pre-H4 (43.3 – 40.2 ky cal BP), H4 (40.2 – 38.6 ky cal BP), and Post-H4 (38.6 – 36.5 ky cal BP) paleoenvironmental reconstructions (Banks et al. 2008b). Ecological niche modeling (ENM) analyses using GARP were performed for 5 different sample designs for the Pre-H4, H4, and Post-H4: 1) samples of Middle Paleolithic (MP) archaeological sites at which diagnostic hominin remains have never been discovered, referred to here as "Middle Paleolithic exclusive," 2) samples of Middle Paleolithic archaeological sites at which diagnostic hominin remains have never been discovered that were tasked with predicting locations of Neandertal remains dating to the same paleoenvironmental reconstruction, referred to as "technocomplex to fossil," 3) samples made up exclusively of the locations of Neandertal fossils, referred to here as "Neandertal exclusive," 4) combined samples of the locations of Neandertal fossils and Middle Paleolithic archaeological sites that have never produced diagnostic hominin remains, referred to as "Neandertal/Middle Paleolithic combined," and 5) samples of Upper Paleolithic archaeological sites, referred to as "Upper Paleolithic exclusive." Each of the preceding 5 types of experiments was repeated for each of the paleoenvironmental reconstructions, using the presence-points described in Section 4.2.

Consensus predictive models take the habitat found at the sites of the samples used and predict the location of similar habitat that is at least as suitable as the original.

The results of each of 4 of the 5 types of experiments described in the preceding paragraph (all but the technocomplex to fossil tests) include 3 types of maps created from the consensus prediction models: 1) the majority consensus prediction map, 2) the minimum consensus prediction map, and 3) the maximum consensus prediction map. As discussed in Section 5.6, the majority consensus prediction maps are those where pixels are classified as present if a majority of the best-subsets models (50% or more) used to create the consensus predictive model label that pixel as present. The minimum consensus prediction maps only display pixels as predicted present if all of the best-subsets models used to create the consensus prediction model classified that pixel as present. The minimum maps are therefore the most conservative view of the consensus prediction models. The maximum consensus prediction maps classify pixels as present if any of the best-subsets models designate the pixel as present. The maximum maps are thus considered to be the least conservative result included in this dissertation.

The results of the technocomplex to fossil experiments include a total of 2 maps. The first is the thresholded prediction map where the Least Presence Threshold (LPT) was used to create a presence/absence prediction map. The second is an unthresholded consensus prediction map which displays the full breadth of the variation in predictions generated by the single best-subsets run. The unthresholded map is displayed as a heat map with 10 discrete colors from blue to red, where each pixel's color corresponds to the number of models that predicted that pixel as present. There are two main benefits for calibrating and testing models in this manner: 1) because these models are tested with a completely different and unique sample than was used to generate them, this consensus

prediction model can be calibrated with the entirety MP Pre-H4 sample of 23 locations rather than a subset as is standard protocol with the other experimental designs included in this study and 2) since a subdivision of the sample into calibration and validation subsets is not required, the sample only needs to be run through GARP once with standard best-subsets procedures. This makes the processing procedures much simpler than is seen in any other standard testing procedure.

In addition to the results of the above experiments, this section also reports the results of the geographic overlap analysis for the Pre-H4, H4, and Post-H4 reconstructions. These analyses directly compare the majority consensus prediction maps for a select number of the total experiments conducted for this dissertation. For the Pre-H4 paleoenvironmental reconstruction, the following overlaps are reported: 1) Neandertal exclusive with Middle Paleolithic exclusive, 2) Neandertal exclusive with Upper Paleolithic exclusive, and 3) Neandertal/Middle Paleolithic combined with Upper Paleolithic exclusive. For the H4 and Post-H4 only the overlap analyses for the Neandertal/Middle Paleolithic combined with the Upper Paleolithic exclusive are reported, due to the extremely small samples sizes of the Neandertal exclusive samples during those time periods. The technocomplex to fossil experiments, where models generated with Middle Paleolithic sites are asked to predict the locations of Neandertal fossil sites, were not included in the overlap analyses because these models are not directly comparable to the other types of experiments which are created and validated with the same sample.

6.1 Pre-H4 (43.3 – 40.2 ky cal BP) Consensus Prediction Models

The results of the consensus prediction models dated to the Pre-H4, from 43.3 – 40.2 ky cal BP (Banks et al. 2008b) are described in Section 6.1: Middle Paleolithic exclusive, technocomplex to fossil, Neandertal exclusive, Neandertal/Middle Paleolithic combined, and Upper Paleolithic exclusive.

6.1.1 Middle Paleolithic Exclusive Consensus Prediction Model

For the Pre-H4 reconstruction, the following predictive maps were produced by a sample of Middle Paleolithic archaeological sites that have never produced diagnostic Neandertal remains (n = 23) (refer to Figures 13 – 15) and were generated with the randomization and splitting/sorting method described in Section 5.3.2, which resulted in 5 replicate runs. For this consensus prediction model, all p-values were $\leq 5.4 \times 10^{-4}$ (Table 14) and all Partial-ROC scores were $\leq 6.1 \times 10^{-4}$ (Table 15). These values indicate that this model predicts known test points at a better than random rate and the null hypothesis that these results occurred due to random chance can be rejected.

The majority consensus prediction map for this model (Figure 13) displays a presence/absence map where pixels classified as present more than 50% of the time are shown in red while pixels classified as absent more than 50% of the time are displayed in blue. The majority map takes a midline approach to displaying the extent of suitable habitat in comparison to the very conservative minimum map and less conservative maximum map. The majority map shows large areas of predicted presence of suitable habitat in the northern Iberian Peninsula, France, parts of central Germany, the Czech

Republic, and Austria. Solid, more continuous predictions of presence occur more frequently in Western and Central Europe. The Ebro River Valley shows areas of predicted presence, though they are most concentrated in the western portion of the valley near the headwaters of the Ebro River. There are also smaller, discontinuous areas of predicted presence in Northern Italy, the Balkan Peninsula, and areas of Romania, Moldova, the Ukraine, and southern Great Britain. Notable areas of absence include the southern extent of the Iberian Peninsula in coastal regions and areas of lower elevation, the Alps, and the Great Hungarian Plain. The presence/absence pixel ratio, where the number of pixels predicted present is divided by the total number of pixels (12,399/58,251), is equal to 21% percent of the area in the map (Table 16). Pixels classified as present are bound between 54 to 37.2 degrees latitude.

The minimum consensus prediction map for the Middle Paleolithic exclusive model during the Pre-H4 is also displayed in presence/absence format (Figure 14). Here pixels are only classified as present if all 5 of the random replicates predict them as present. This is the most conservative and most geographically restricted prediction out of all maps generated for the MP Pre-H4 sample. There are only 2,143 pixels were predicted present, or 4% of the total study area (Table 16). The minimum prediction shows a much smaller and more geographically constricted area of predicted presence. Here pixels indicating presence of similar habitat found at the sample locations are bound by latitudes of 48.5 and 40.25 degrees. Areas predicted present in this map are concentrated in the northern Iberian Peninsula (including the western and central portions of the Ebro River Valley) and central to southern France. Some scattered areas

through the Dinaric Alps are also identified by the minimum consensus prediction map as areas where similar suitable habitat is present.

The maximum thresholded prediction is the least conservative examination of the consensus prediction for the Middle Paleolithic exclusive sample dating to the Pre-H4 (Figure 15). If a pixel was ever predicted as present by any of the 5 replicate runs, it was included here as present. 32,315 pixels were predicted as present, or 55% of the total study area (Table 16). The maps shows predicted presence across the majority of western and central Europe between 55.5 and 36.75 degrees latitude, excluding the Alps and portions of southwestern Iberia, similar to the majority map. Many of the geographic areas shown on the majority map are also shown here, but with a higher density of pixels predicted present. The maximum extent of suitable habitat reaches up into the northernmost reaches of Germany, Poland, and Belarus, and south to Sardinia, Greece (including the Peloponnese), and southern Turkey.

Please refer to Tables 15 – 16 for results of statistical validation and pixel counts.

Evaluation replicates	***p*-values**	**Critical Binomial Values**	**Success rates**
Evaluation set 1	2.904×10^{-8}	5	0.91
Evaluation set 2	5.43267×10^{-4}	5	0.64
Evaluation set 3	4.73956×10^{-6}	4	0.73
Evaluation set 4	2.80338×10^{-4}	2	0.36
Evaluation set 5	4.05113×10^{-5}	5	0.73

Table 14. Results of the statistical validation procedures using cumulative binomial probability and critical binomial value tests for the Middle Paleolithic exclusive consensus prediction model during the Pre-H4.

	1	2	3	4	5
Minimum	1.633851	1.156616	1.165775	1.001567	1.312651
Maximum	1.793224	1.775392	1.829461	1.939112	1.781043
Mean	1.764047	1.547454	1.674278	1.569335	1.622655
SD	0.037126	0.133318	0.122802	0.176135	0.103502
Replicates ≤ 1	0	0	0	0	0
Z-statistic	650.7884	129.8550	174.0581	102.2166	190.2382
P	2.085×10^{-94}	2.010×10^{-5}	1.854×10^{-8}	6.138×10^{-4}	8.957×10^{-10}

Table 15. Partial-ROC scores for the Pre-H4 Middle Paleolithic exclusive model.

	Pixels predicted present	Pixels predicted absent	Ratio of present/total
Majority	12,399	45,852	0.21
Minimum	2,143	56,108	0.04
Maximum	32,315	25,936	0.55

Table 16. Pixel ratios for the Pre-H4 Middle Paleolithic exclusive majority, minimum, and maximum consensus prediction maps.

The majority, minimum, and maximum consensus prediction maps for the Pre-H4 Middle Paleolithic exclusive model begin on the next page (Figures 13 – 15).

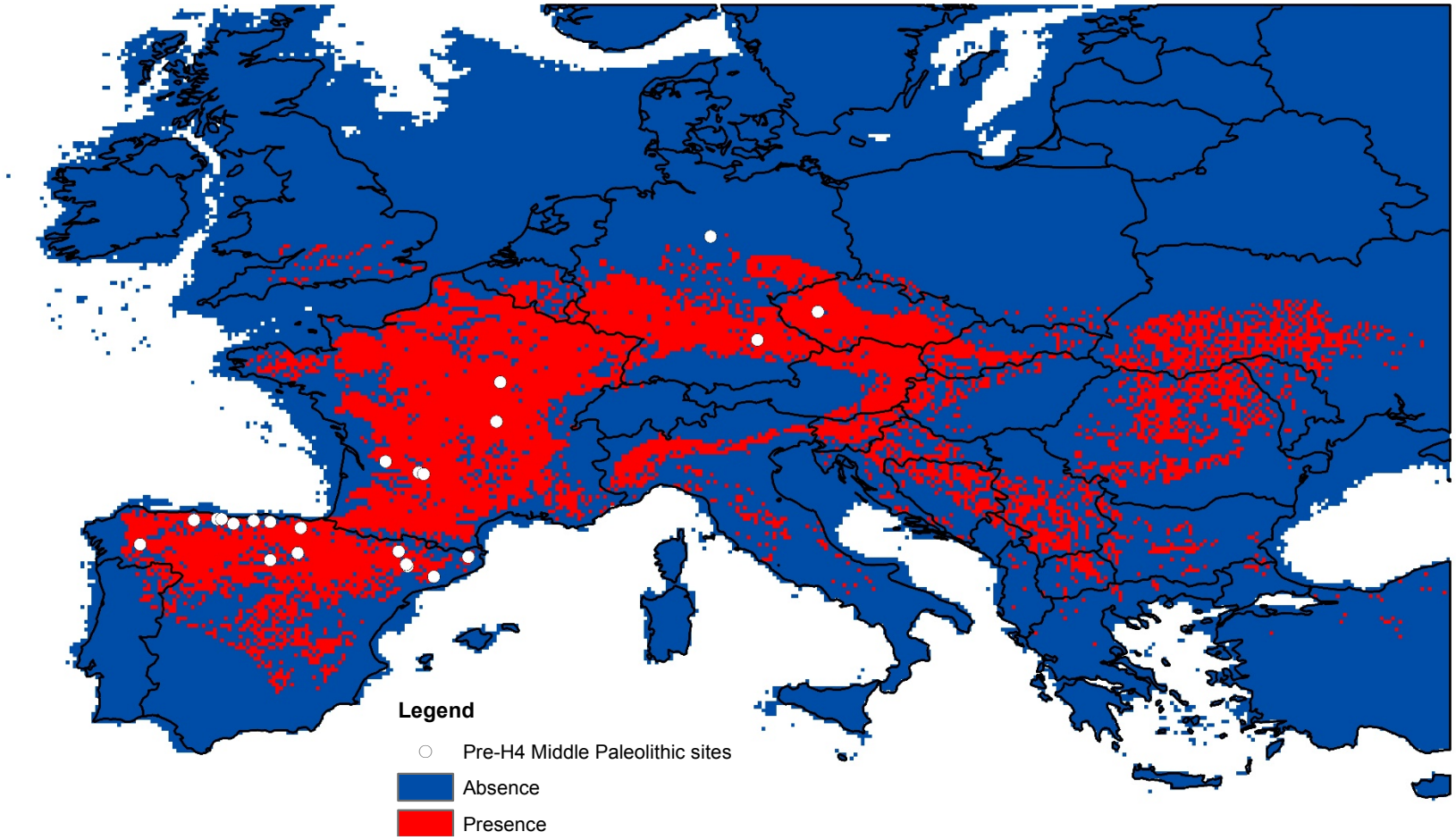

Figure 13. Majority consensus prediction map for the Pre-H4 Middle Paleolithic exclusive.

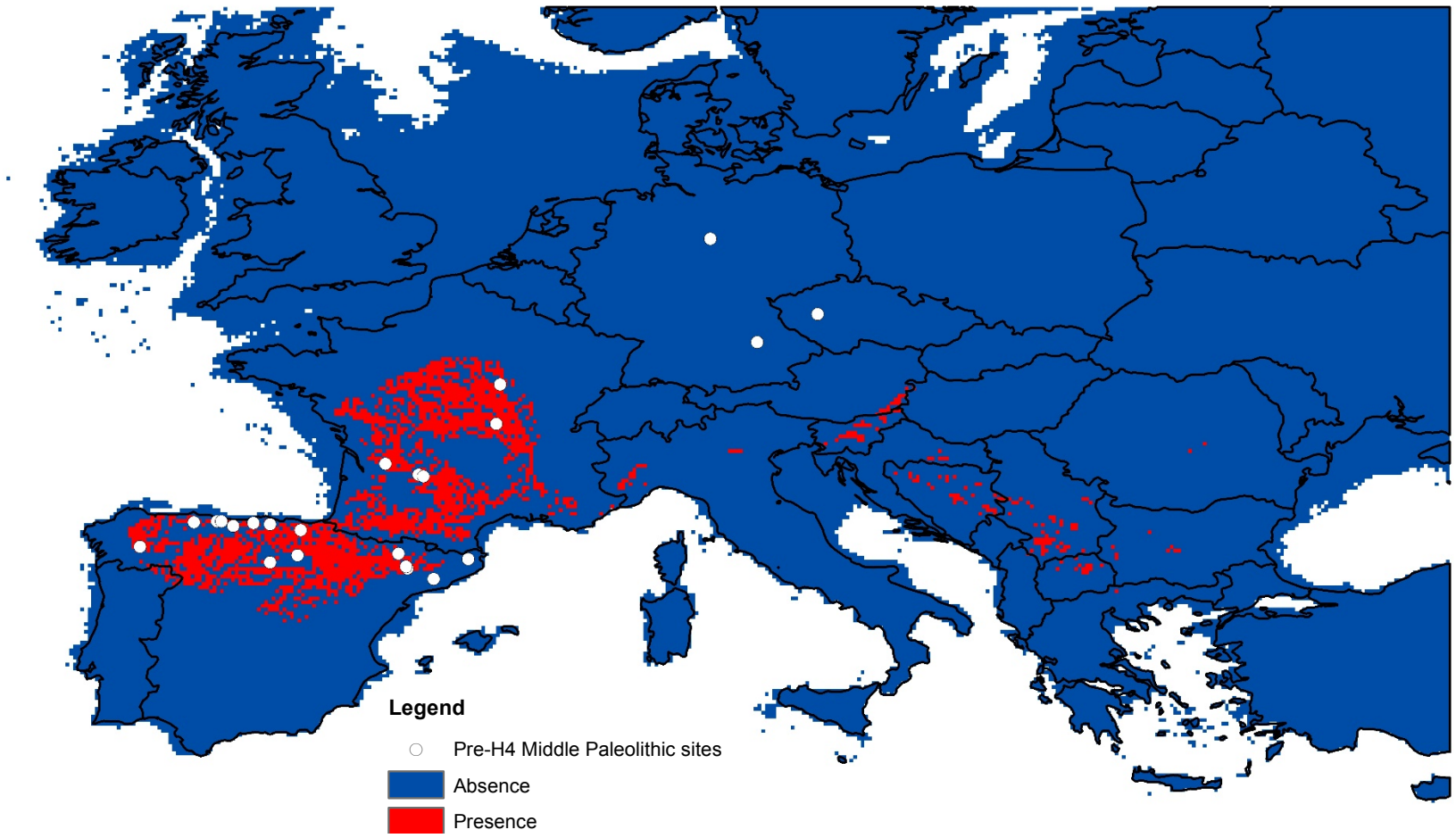

Figure 14. Minimum consensus prediction map for the Pre-H4 Middle Paleolithic exclusive model.

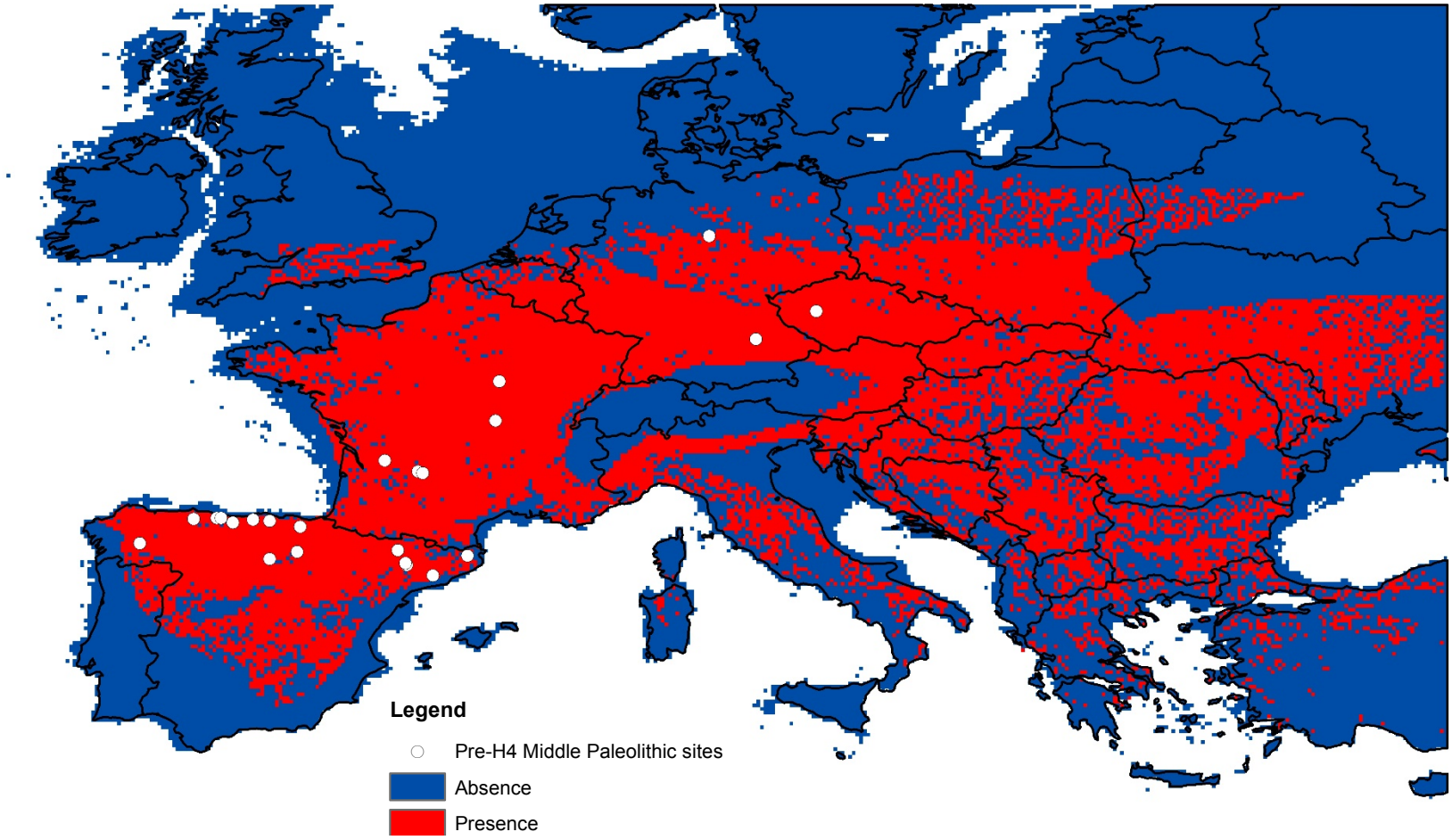

Figure 15. Maximum consensus prediction map for Pre-H4 Middle Paleolithic exclusive model.

6.1.2 Technocomplex to Fossil Consensus Prediction Model for Middle Paleolithic Archaeological Sites and Neandertal Fossil Locations

For the Pre-H4 paleoenvironmental reconstruction, the following consensus prediction model maps (Figures 16 and 17) were produced by a sample of Middle Paleolithic archaeological sites at which no diagnostic Neandertal remains have been found (n = 23), but tested for that model's ability to correctly classify the locations of Neandertal fossils dating to the same period (n = 14). The p-value of the thresholded prediction was calculated using a cumulative binomial probability and returned a significant value of p = 0.04 and a critical binomial value of 7.

Both the thresholded and un-thresholded predictions for this model show the majority of the areas predicted as present falling between 54 to 37.2 degrees latitude (as was seen in the previous Middle Paleolithic exclusive results during the Pre-H4). The predictions show large areas with suitable habitat presence in northern and central Iberia, much of present-day France, the head of the Po River Valley, the central Apennine Peninsula, the Dinaric Alps, the Balkan Peninsula, the Carpathians, the area north of the Alps (portions of Belgium, south and central Germany, Austria, the Czech Republic, and Poland), as well as some isolated pixels in southern Great Britain and the Republic of Ireland. Interestingly, this model does not show the presence of correlated environmental variables in southern Iberia and the Great Hungarian Plain.

The success rate of the model in correctly classifying the known Neandertal locations in the validation sample was 50%, or 7 out of 14 test points. The thresholded results produced a consensus model that predicted known test points at a better than

random rate and the null hypothesis of these results occurring due to random chance can be rejected. 17,805 pixels were predicted present by all 10 best-subsets models, or 31% of the total study area. 19,999 pixels, or 34% of the study area, were classified as absent by all 10 models chosen by the best-subsets procedures.

In contrast to the thresholded results, the results of the Partial-ROC test on the unthresholded consensus prediction resulted in a *p*-value of 0.24, where 202 of the 1,000 bootstrap replicates returned a value of ≤ 1. This indicates that the null hypothesis cannot be rejected. In other words, this unthresholded consensus prediction which takes into account the full range of predictions from each of the 10 models in the best-subsets run could ***not*** be demonstrated to predict the test points at a better than random rate. The consensus prediction model created by this experiment to address the ability of Middle Paleolithic archaeological sites to predict locations of Neandertal remains was only able to do so when standard Least Presence Threshold practices (LPT) were used to designate which pixels were classified as present and which were classified as absent.

In other words, when the full range of results generated by the best-subsets for predicting the presence of suitable habitat was included, the results shown in Figure 17 could be due to random chance. This is the only technocomplex to fossil consensus model generated for this dissertation that produced results where the thresholded version of the model predicted test points at a better than random rate while the unthresholded version did not. Considering the difference found between the cumulative binomial probabilities and the Partial-ROC test, during the Pre-H4, a model that was calibrated with Middle Paleolithic archaeological sites cannot predict the locations of

morphologically diagnostic Neandertal fossil remains with complete confidence. This indicates that there is some level of disconnect between the habitats found between this sample of archaeological sites that have never produced hominin remains and the habitats found associated with the fossil remains of their probable creators.

P	0.04
Critical Binomial Value	7
Test points correctly classified as present	7
Success rate	0.50

Table 17. Validation results for the thresholded Pre-H4 technocomplex to fossil model.

Minimum	0.57
Maximum	1.69
Mean	1.18
SD	0.24
Replicates ≤ 1	197
Z-statistic	24.05
P	0.24

Table 18. Partial-Roc validation for the Pre-H4 technocomplex to fossil model.

The thresholded and unthresholded prediction maps (Figures 16 and 17) for the Pre-H4 technocomplex to fossil consensus prediction model begin on the following page. Please refer to Tables 17 and 18 for the results of the statistical validation tests.

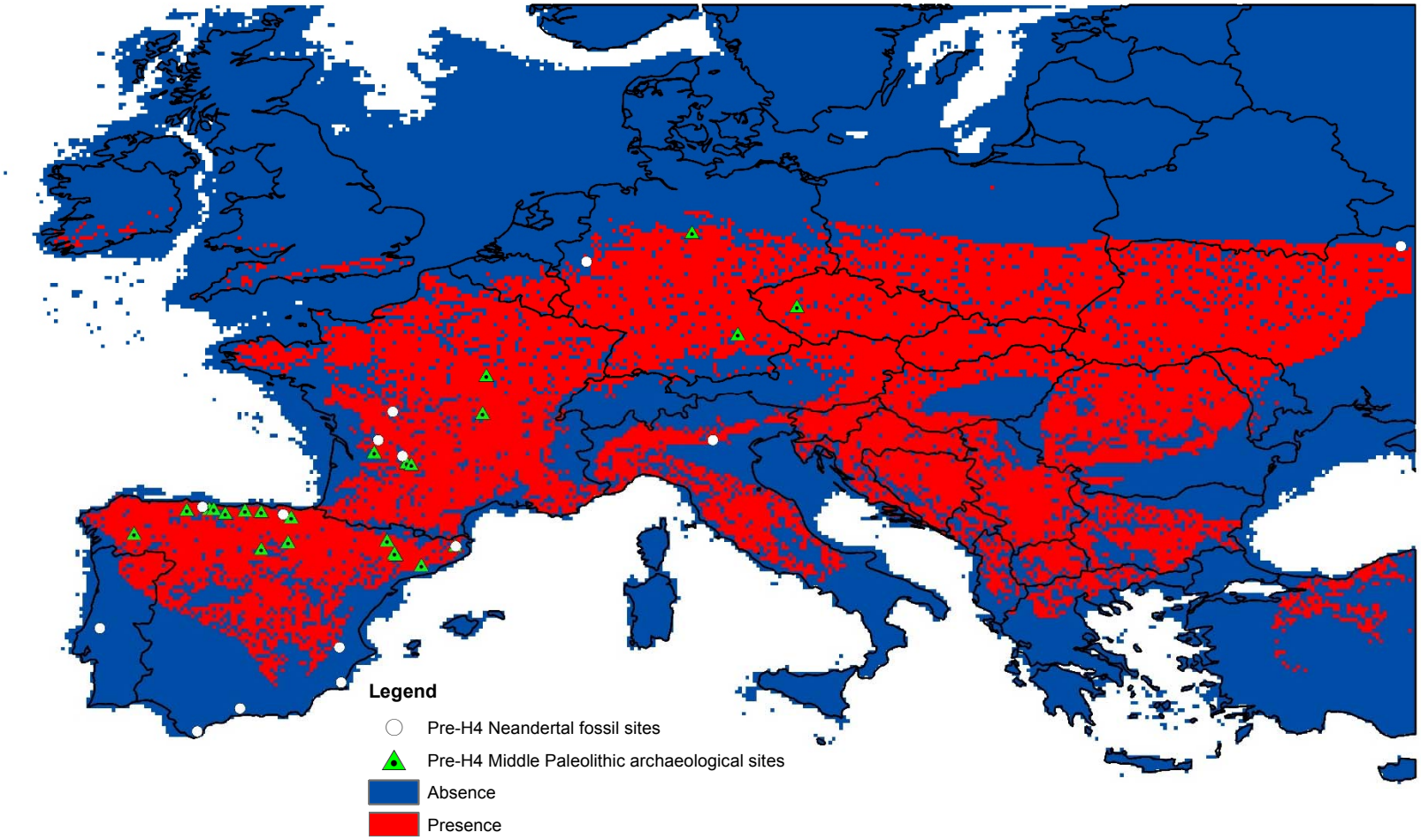

Figure 16. Thresholded consensus prediction map for the technocomplex to fossil model generated with Middle Paleolithic archaeological sites (*n* = 23) and validated Neandertal fossil locations (*n* = 14) for the Pre-H4.

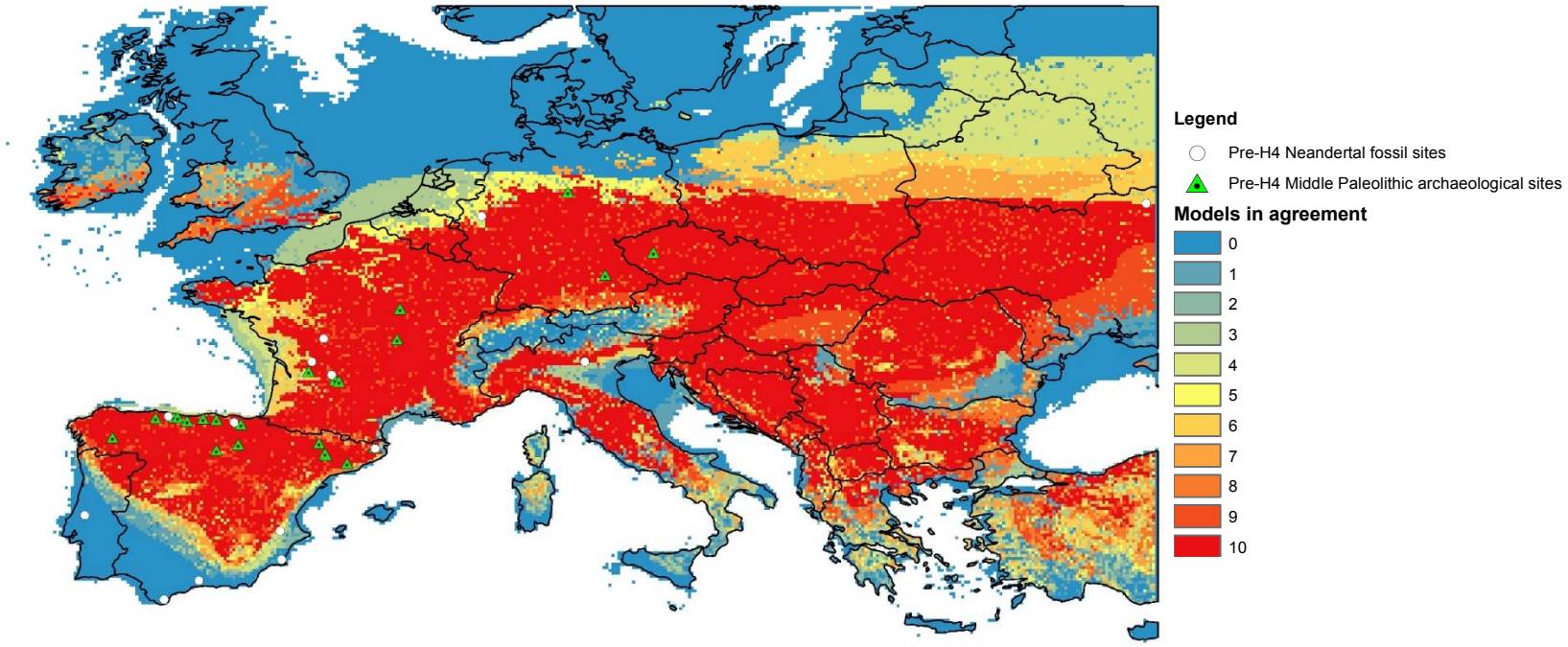

Figure 17. Unthresholded consensus prediction map for the technocomplex to fossil model generated with Middle Paleolithic archaeological sites (*n* = 23) and validated Neandertal fossil locations (*n* = 14) for the Pre-H4.

6.1.3 Neandertal Exclusive Consensus Prediction Model

Majority, maximum, and minimum consensus prediction maps were generated for the Neandertal exclusive sample dating to the period of 43.3 – 40.2 ky cal BP (n = 14), during the Pre-H4 paleoenvironmental reconstruction (see Figures 18 – 20). The model was calibrated and tested using the $n - 1$ procedure described in Section 5.3.1. For this model, $p = 0.02$ (via the Pearson's P-Value Compute program) and a success rate of 57%, with 8 out of 14 test points classified correctly (Table 19). This indicates that the model is able to predict known test points at a better than random rate and the null hypothesis that these results are due random chance can be rejected.

The majority map (Figure 18), where at least 50% of the $n - 1$ replicate models (7 or more models) are in agreement, classified 17,248 (30% of the study area) as present (Table 20) and shows the pixels bound between 52 and 36 degrees latitude. The areas of highest concentration of pixels predicted present are located in modern Ukraine, portions of the Balkan Peninsula, the Apennine Peninsula, Sardinia, western France, southern England, the Great Hungarian Plain, the Dnieper Uplands, and the Iberian Peninsula including the Ebro River Valley. This model, which includes Neandertal locations south of the Ebro River that have been dated to this time period, is the first in this project that predicts pixels as present in the southern extremes of the Iberian Peninsula. The area immediately north of the Alps is largely predicted as absent and the southern Carpathian Mountains and Dinaric Alps show fewer areas predicted as present than seen in the predictions generated from the previous models discussed for the Pre-H4.

The minimum prediction for this model (Figure 19) is the most theoretically conservative map and classified only 6,233 (11% of the study area) as present (Table 20). The pixels for the minimum prediction are more latitudinally constrained in a southward direction when compared to the majority map. All pixels predicted present on this map fall south of 49 degrees latitude. The minimum prediction displays 19% less of the total study area as present than the majority prediction. The concentration of pixels predicted present are also less continuous and "patchier" in nature in comparison. Despite the extremely restricted areas of predicted presence, the Ebro River Valley does show areas of probable presence, along with the Po River Valley, the Great Hungarian Plain, the Dnieper Uplands, and Turkey.

The maximum consensus prediction map (Figure 20), where pixels are displayed in red if they were ever classified as present by any of the 13 replicates used to build the model, showed 26,130 as present (49% of the total study area) (Table 20). This is 19% more than the majority prediction and 38% more than the minimum prediction. High concentrations of probable presence are seen in modern France, the Iberian Peninsula, the Apennine Peninsula, the Balkan Peninsula, and the Anatolian Peninsula. The maximum consensus prediction map also includes a much greater area of suitable habitat agreed upon by one or more replicates in coastal areas that are currently under water. These areas include the paleo-shorelines surrounding the majority of the Iberian Peninsula, France, the Adriatic shelf, the Black Sea shelf, and areas under the English Channel. The maximum map also identifies scattered pixels in northern Germany as present.

P	0.02
Success ratio	0.57

Table 19. Pearson's *p*-value results for the Pre-H4 Neandertal exclusive model.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	17,248	41,003	0.30
Minimum	6,233	52,018	0.11
Maximum	26,130	32,121	0.49

Table 20. Pixel ratios for the Pre-H4 Neandertal exclusive predictions.

The majority, minimum, and maximum consensus prediction maps for the Pre-H4 Neandertal exclusive consensus model (Figures 18 – 20) begin on the following page.

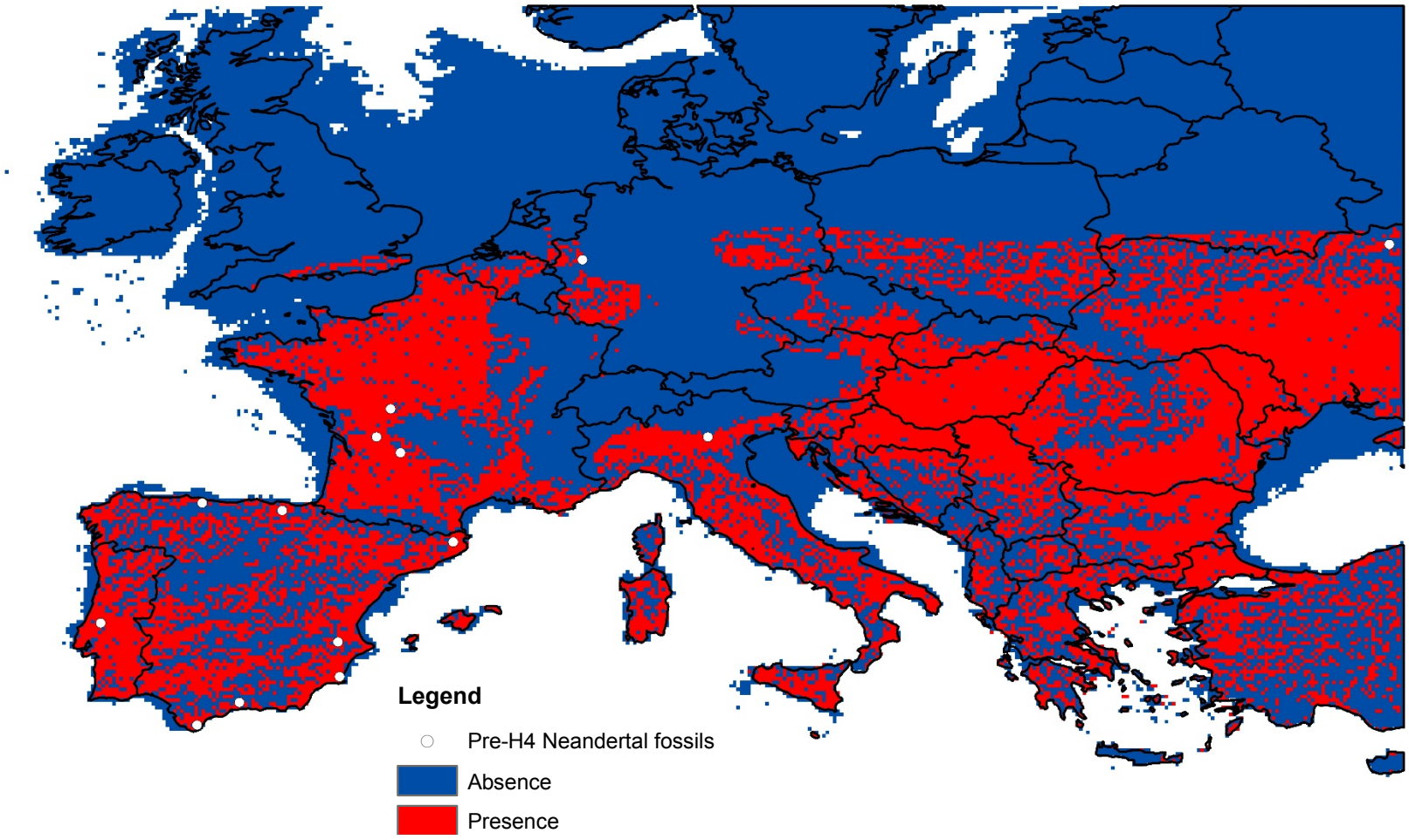

Figure 18. Majority consensus prediction map for the Pre-H4 Neandertal exclusive model.

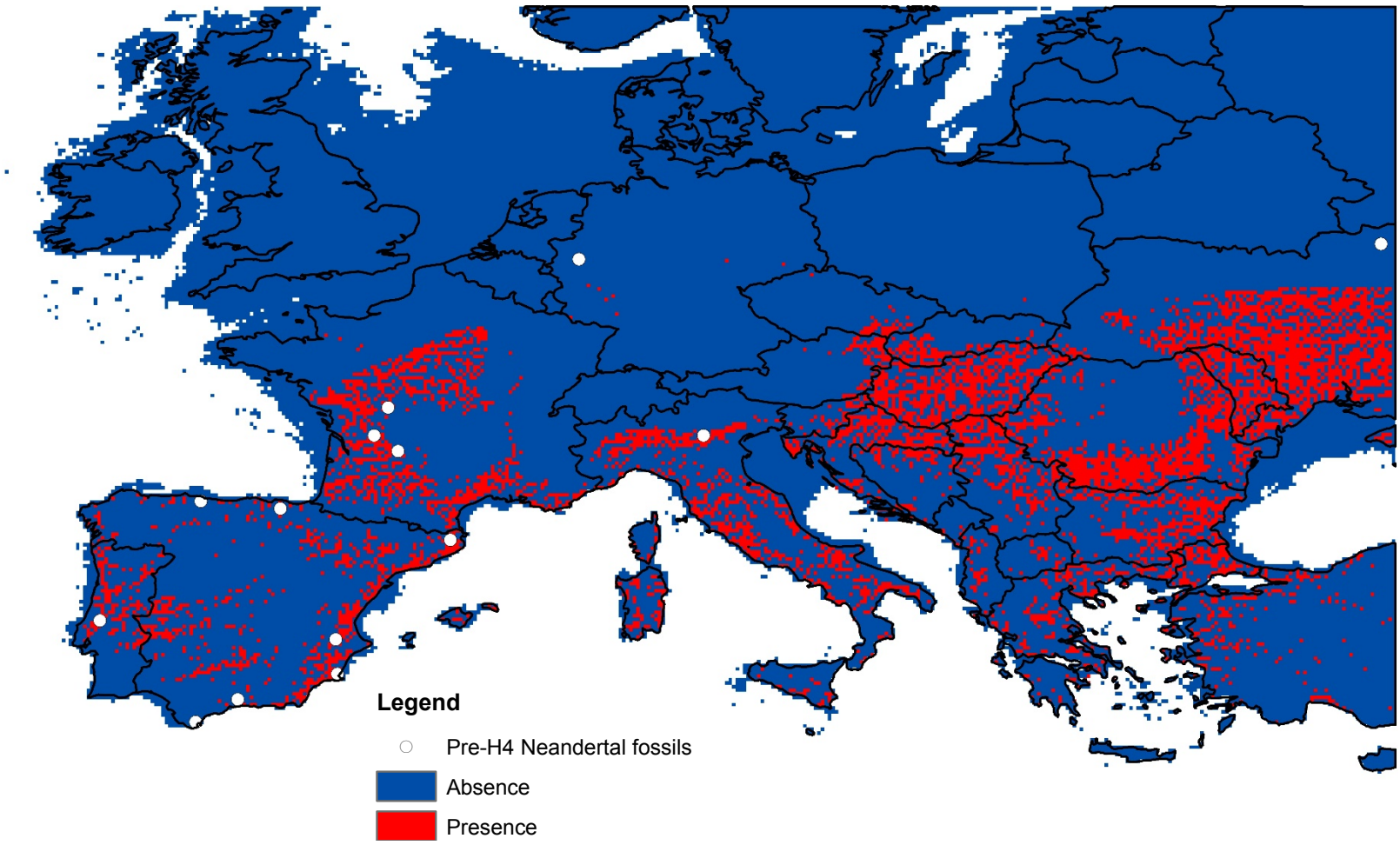

Figure 19. Minimum consensus prediction map for the Pre-H4 Neandertal exclusive model.

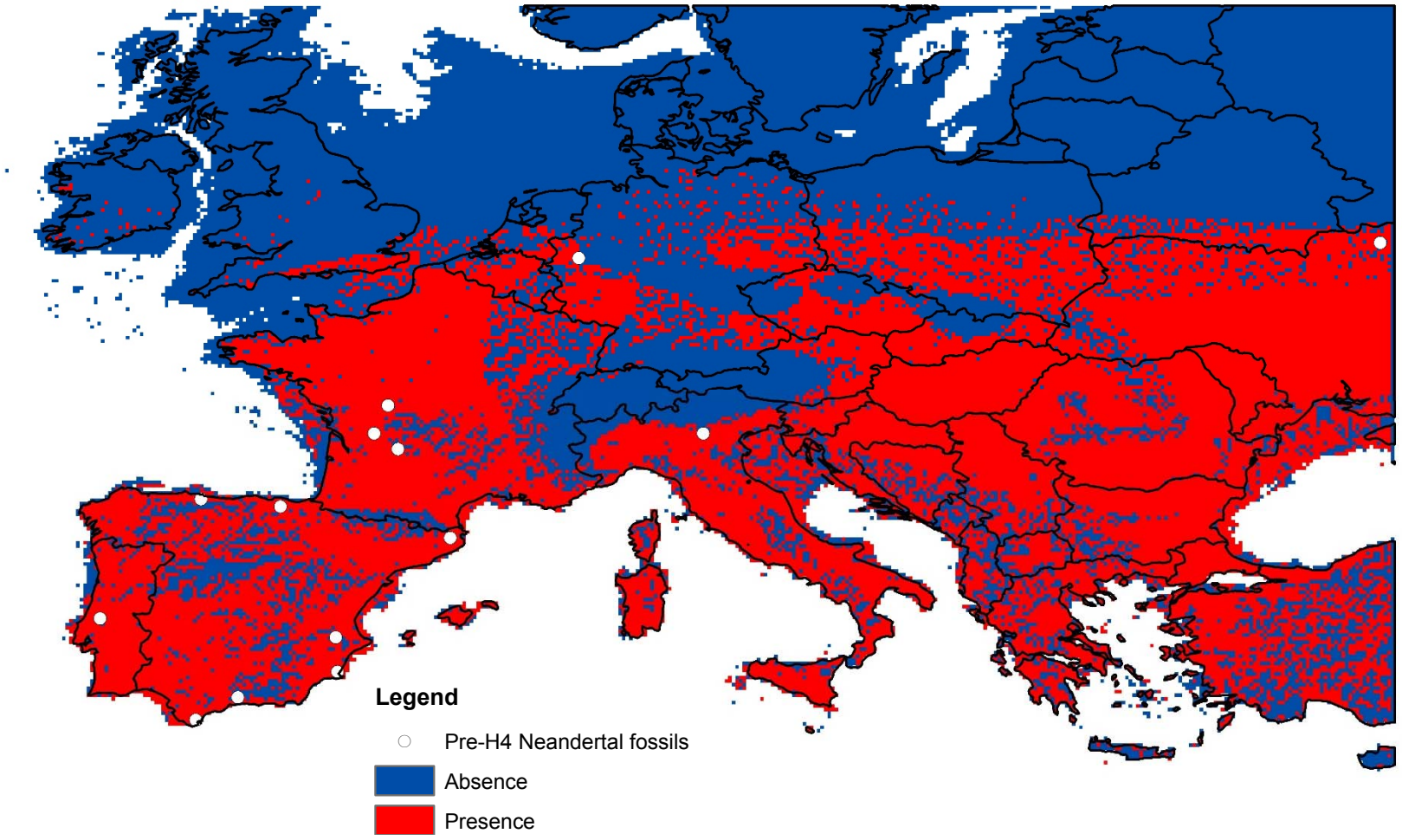

Figure 20. Maximum consensus prediction map for the Pre-H4 Neandertal exclusive model.

6.1.4 Neandertal Fossil and Middle Paleolithic Archaeological Combined Sample

For the combined sample of Neandertal fossil and Middle Paleolithic archaeological sites during the Pre-H4 (n = 37) majority, minimum, and maximum consensus prediction maps were generated for the consensus model using the randomization and splitting/sorting method. All p-values calculated with cumulative binomial probabilities were $\leq 6.5 \times 10^{-4}$ and Partial-ROC scores were ≤ 0.008 (Table 21 and 22). These values indicate that this model predicts known test points at a better than random rate and that this consensus model is not the result of random chance.

The area predicted as present on the majority consensus prediction map (Figure 21) is bounded by latitudes of 36.8 and 52.8 degrees north. Iberia, including the Ebro River Valley and Meseta Central, shows a large area of suitable habitat, except for the southwestern corner of the peninsula. Other significant areas of predicted presence include the majority of France, Sardinia, the Apennine Peninsula, Sicily, the Great Hungarian Plain, the Balkan Peninsula, Dinaric Alps, the Anatolian Peninsula, and areas north of the Alps. Interestingly, the Carpathian Mountains are also shown to have large areas of habitat similar to the sample. The areas predicted present cover 35% of the study area (20,575 pixels) (Table 23).

The more conservative minimum consensus prediction map (Figure 22) classifies 14% of the pixels in the study area as present (8,076 pixels) (Table 23). When all thresholded best-subset runs used to create the consensus prediction are in agreement, 21% less of the study area is predicted to have highly suitable habitat for this sample during the Pre-H4. Areas marked present here include the Ebro River Valley, scattered

pixels across northwestern Iberia and the southern portions of the Meseta Central, central France, the Po River Valley, the central Apennine Peninsula, the Great Hungarian Plain, the Balkan Peninsula, the Dnieper Uplands and other lowland areas surrounding the Carpathian Mountains, plus scattered areas in northern Anatolia, Austria, the Czech Republic, Germany, and Belgium. The outline of the Carpathian Mountains becomes slightly more apparent in the minimum consensus prediction map.

In the maximum prediction map (Figure 23), the least conservative of the three reported here, 49% of the study area (28,403 pixels) is classified as present (Table 23). The prediction is similar to the majority map, with a few notable differences. The total area classified as present is much more continuous than was seen in the majority or minimum maps and the latitudinal bounds of the area is increased to 53.8 and 36 degrees. A few scattered pixels through the southern Republic of Ireland, southern Wales, and southern and central England, and northern Germany increase the northern boundary of the prediction. This is the only map for this sample during the Pre-H4 to predict the southern extremes of Iberia as present. The major mountain chains of Europe, except for the Alps, cease to be distinct areas of absence.

The only lowland areas left out of the maximum consensus prediction map are those that are under water today, including the Adriatic shelf, the English Channel, and the shallow areas of the northern Black Sea. It is likely that these areas would have been predicted present even with the minimum maps if sufficient data indicated Neandertal presence in those areas. However, that data may never be available considering it is now under water.

Evaluation replicates	Cumulative binomial probabilities	Critical binomial values	Success ratios
Evaluation set 1	$1.2x10^{-5}$	10	0.79
Evaluation set 2	$6.5x10^{-4}$	8	0.58
Evaluation set 3	$1x10^{-5}$	11	0.84
Evaluation set 4	$1.8x10^{-7}$	9	0.84
Evaluation set 5	$1x10^{4}$	10	0.74

Table 21. Results of the statistical validation procedures using cumulative binomial probabilities and critical binomial values for the Neandertal/Middle Paleolithic combined consensus prediction model during the Pre-H4.

	1	2	3	4	5
Minimum	1.26	0.73	1.32	1.29	1.08
Maximum	1.65	1.74	1.73	1.69	1.70
Mean	1.53	1.37	1.59	1.59	1.49
SD	0.08	0.16	0.09	0.08	0.11
Replicates ≤ 1	0	11	0	0	0
Z-statistic	216.00	75.86	219.25	246.69	134.91
P	$4.23x10^{-12}$	0.008	$2.06x10^{-12}$	$3.07x10^{-15}$	$9.93x10^{-6}$

Table 22. Results of the Partial-ROC tests for the combined Neandertal/Middle Paleolithic sample during the Pre-H4.

	Pixels predicted present	Pixels predicted absent	Ratio of present/total
Majority	20,575	37,676	0.35
Minimum	8,076	50,175	0.14
Maximum	28,403	29,848	0.49

Table 23. Pixel ratios for the combined Neandertal/Middle Paleolithic sample consensus model during the Pre-H4.

The majority, minimum, and maximum consensus prediction maps for the Pre-H4 Neandertal/Middle Paleolithic combined begin on the next page.

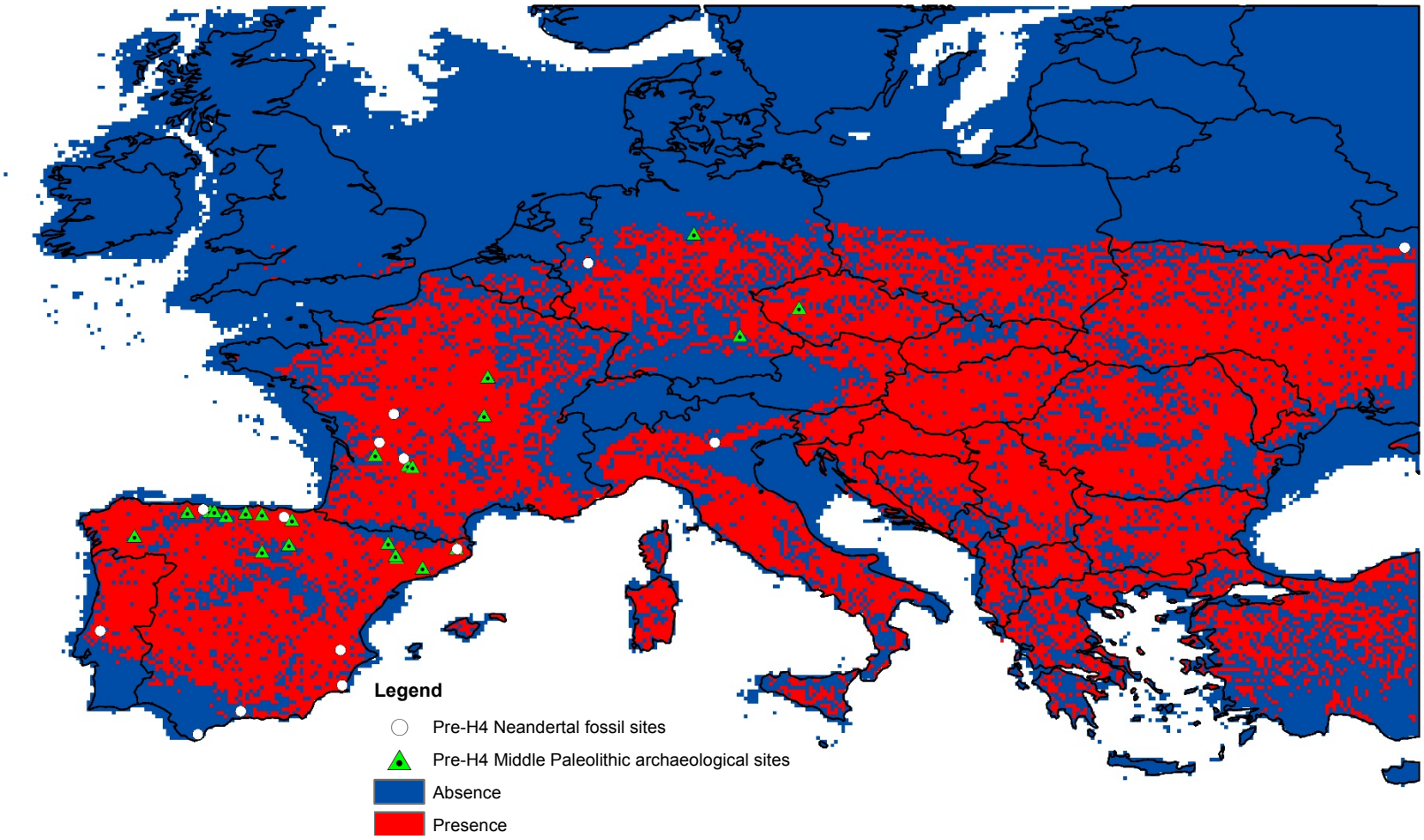

Figure 21. Majority consensus prediction map for the combined sample of Neandertal fossil locations (*n* = 14) and Middle Paleolithic archaeological sites that have not produced morphologically diagnostic hominin remains (*n* = 23) for the Pre-H4.

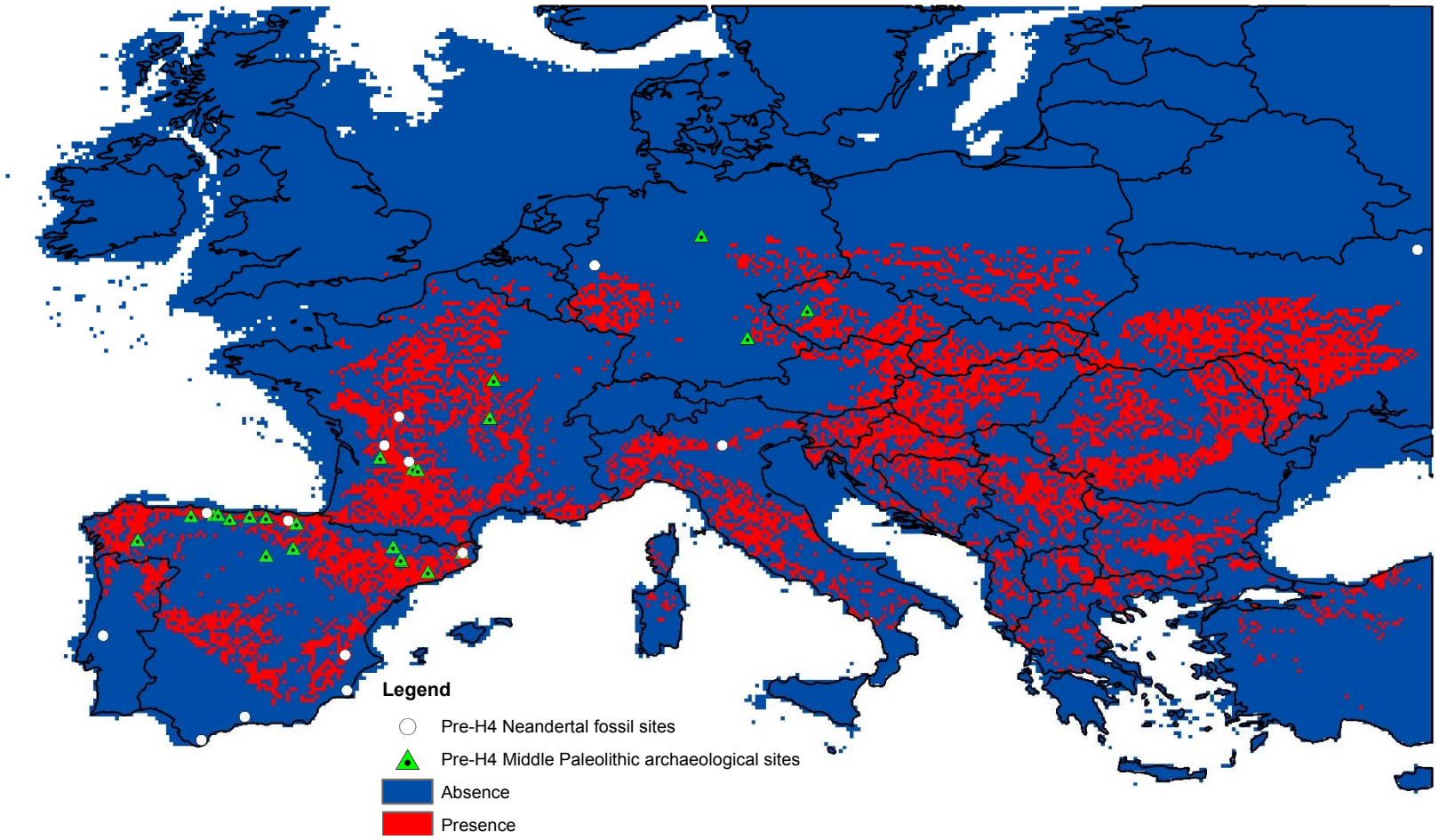

Figure 22. Minimum consensus prediction map for the combined sample of Neandertal fossil locations (*n* = 14) and Middle Paleolithic archaeological sites that have not produced morphologically diagnostic hominin remains (*n* = 23) for the Pre-H4.

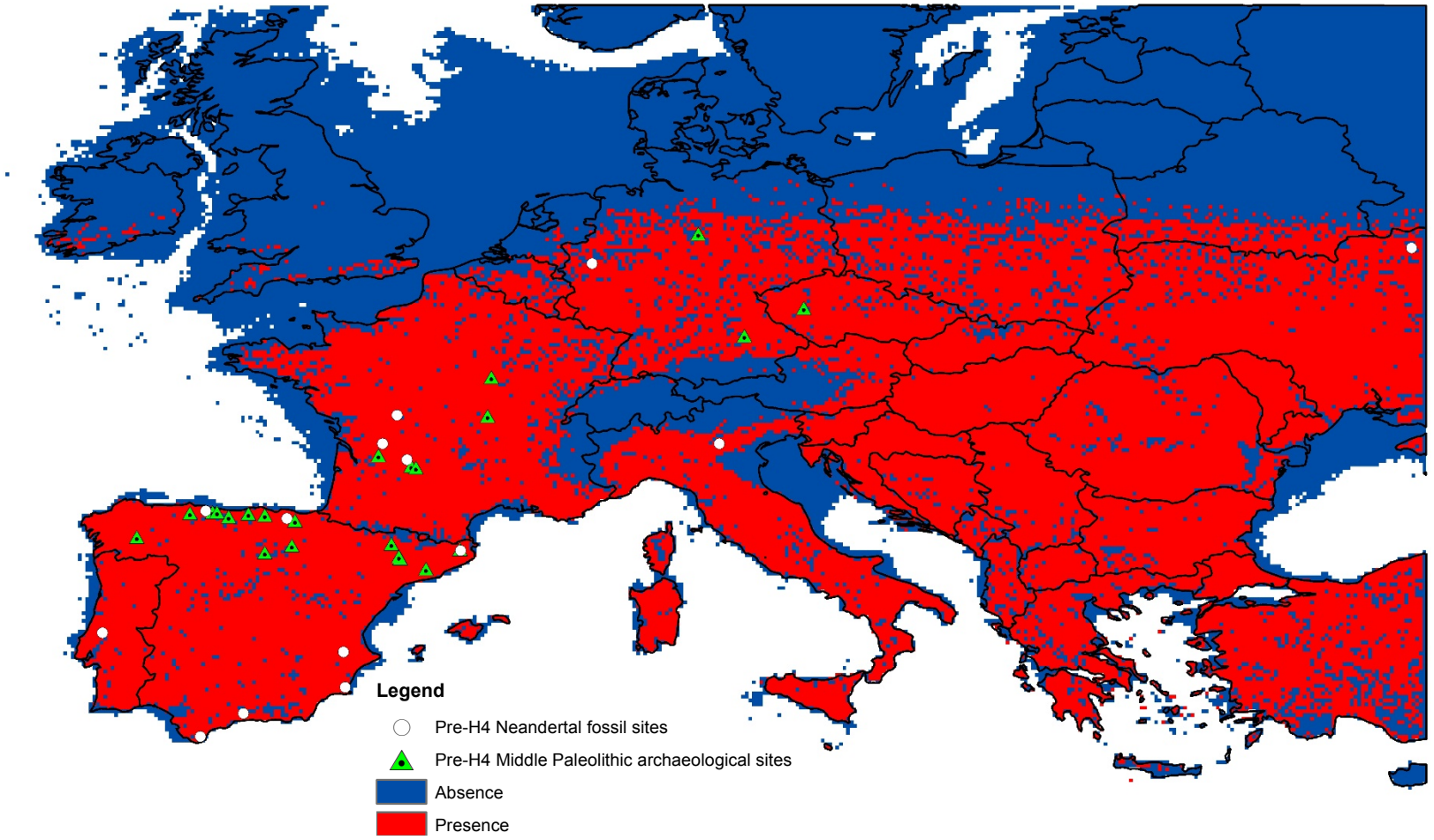

Figure 23. Maximum consensus prediction map for the combined sample of Neandertal fossil locations (*n* = 14) and Middle Paleolithic archaeological sites that have not produced morphologically diagnostic hominin remains (*n* = 23) for the Pre-H4.

6.1.5 Upper Paleolithic Exclusive Consensus Prediction Model

The following predictive model for the Pre-H4 paleoenvironmental reconstruction was calibrated with a sample of locations of absolutely dated Upper Paleolithic archaeological sites (n = 17) and validated with the n – 1 procedure detailed in section 5.3.1. Pearson's P-value Compute (Pearson et al. 2007) was used to calculate a consensus p-value of $p = 6.3\text{x}10^5$ and a success rate = 0.71 for the model (Table 24). This p-value is applicable to all of the predictive maps created from this model. The success rate demonstrates that the model predicted the omitted test point in 12 out of the 17 trials. This indicates that the model is able to predict known test points at a better than random rate and the null hypothesis that these results are due to random chance can be rejected.

The majority map (Figure 24) shows the pixels predicted present, indicating the presence of suitable habitat similar to those found at the sites used to generate the model, are restricted between 51.5 and 37.2 degrees latitude and cover 25% of the total study area (14,432 pixels) (Table 25). The largest concentrations of pixels predicted present are seen in modern France, northern and central Iberia (including the Ebro River Valley), the highland areas just north of the Alps in southern Germany, the Po River Valley, scattered portions of the Apennine Peninsula, Sardinia, the Great Hungarian Plain, portions of the Balkan and Anatolian Peninsula, and the lowland areas immediately to the south and east of the Carpathian Mountains. The Ebro River Valley is clearly shown as a large area of probable presence, with the majority of the valley shown in a continuous area of presence. The only area of the Iberian Peninsula predicted as absent is

the southernmost extreme of the peninsula, south of the Meseta Central. Interestingly, in contrast to all the previous samples meant to model Neandertals, the Upper Paleolithic exclusive model for the Pre-H4 includes portions of the area now under the English Channel and western coast of France.

When the minimum prediction (Figure 25) is examined for the Pre-H4 Upper Paleolithic exclusive consensus model, only 9% of the total study area was predicted as present (5,122 pixels) (Table 25). The pixels predicted present by all 17 $n - 1$ replicates are more latitudinally restricted than seen in the majority map. Here, they are constrained between 50.8 and 39.4 degrees latitude. The highest concentrations of areas predicted present in this highly conservative prediction include large areas of modern France, lowland areas immediately to the east of the Alps (the westernmost Great Hungarian Plain), portions of the Po River Valley, the lowland areas to the south of the Carpathians, the majority of the Ebro River Valley and scattered areas in northwestern and central Iberia.

The least conservative prediction for this model, the maximum consensus prediction map (Figure 26), classifies 44% of the study area as present (25,680 pixels) (Table 25). The pixels are less latitudinally constrained and appear between 52.3 and 36.2 degrees. Most of the study area between these latitudes is predicted as present, with only the Alps and the southernmost extreme of the Iberian Peninsula predicted as absent. The extent of the Alps is sharply defined and the Carpathian Mountains and Dinaric Alps become less visible. Scattered areas in southwestern Ireland, England, Sardinia, Sicily, the Balkan Peninsula, and the Anatolian Peninsula are also predicted as present. It

is in this maximum prediction map that more areas on the Adriatic Shelf and the shallow areas of the Black Sea are also shown as areas of suitable habitat.

P	0.000063
Success rate	0.71

Table 24. Pearson's *p*-value for the Pre-H4 Upper Paleolithic exclusive model.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	14,432	43,819	0.25
Minimum	5,122	53,129	0.09
Maximum	25,680	32,751	0.44

Table 25. Pixel ratios for the Pre-H4 Upper Paleolithic exclusive predictions.

The majority, minimum, and maximum consensus prediction maps for the Upper Paleolithic exclusive sample during the Pre-H4 begin on the following page.

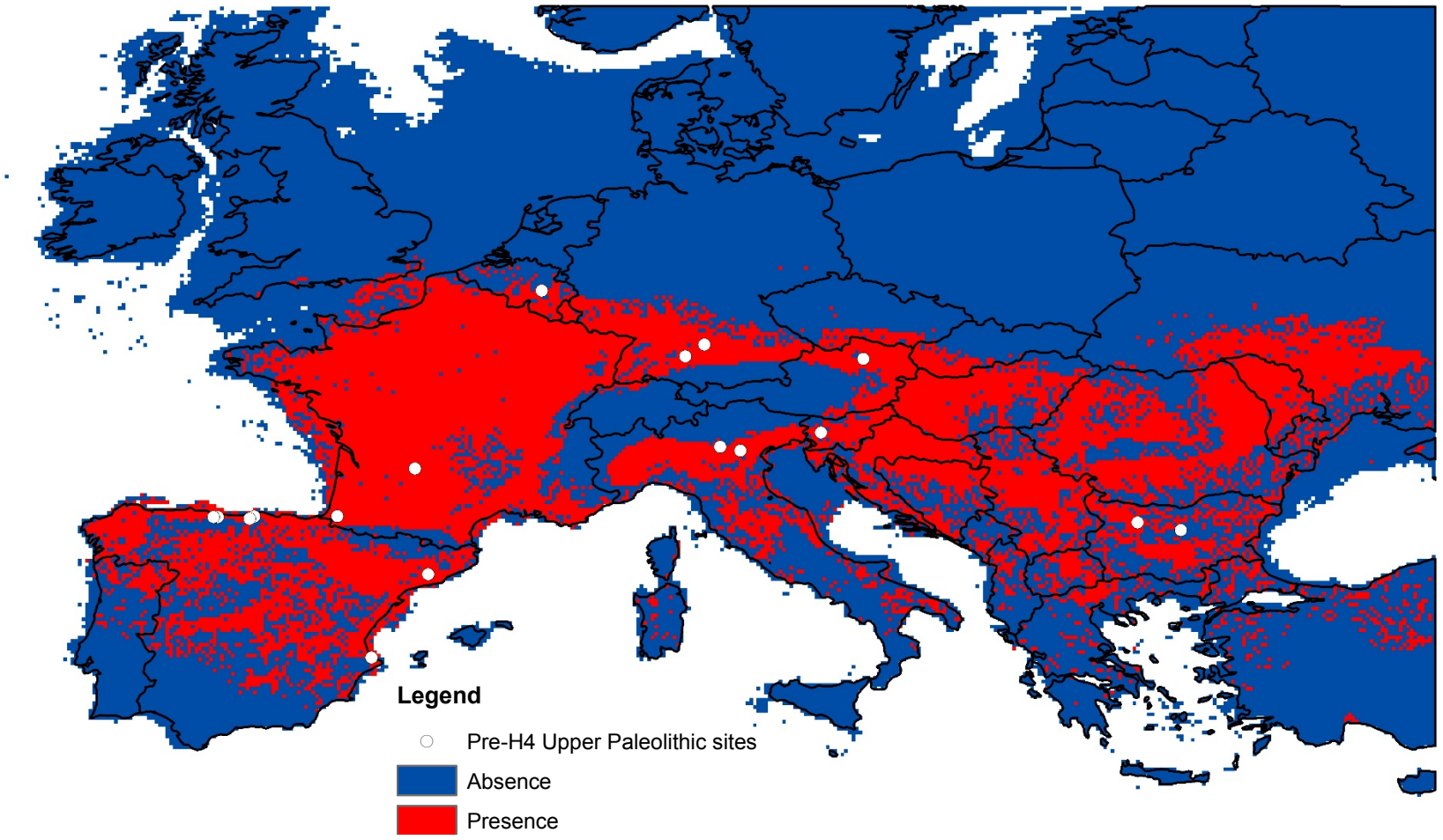

Figure 24. Majority consensus prediction map for the Pre-H4 Upper Paleolithic exclusive model.

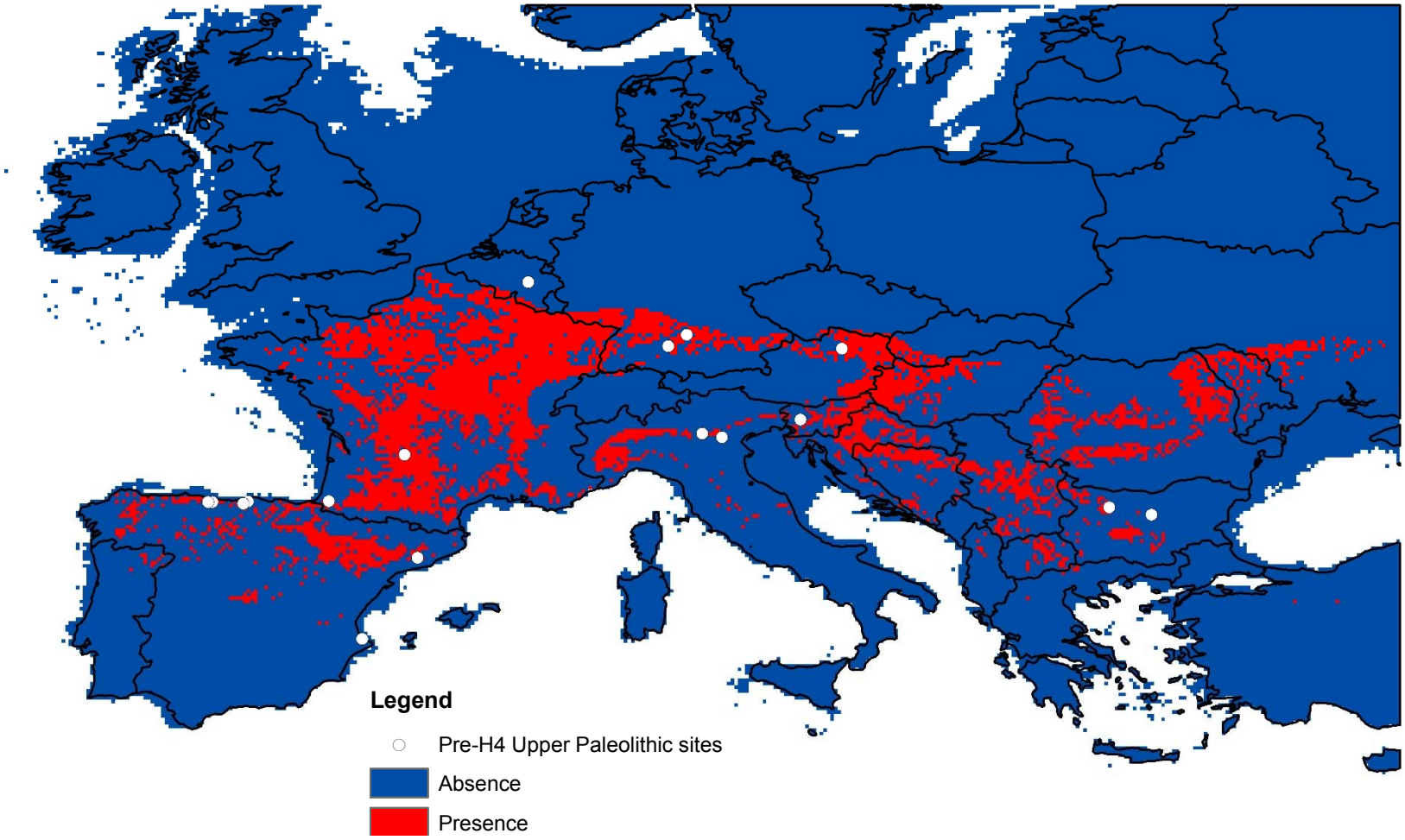

Figure 25. Minimum consensus prediction map for the Pre-H4 Upper Paleolithic excluxive model.

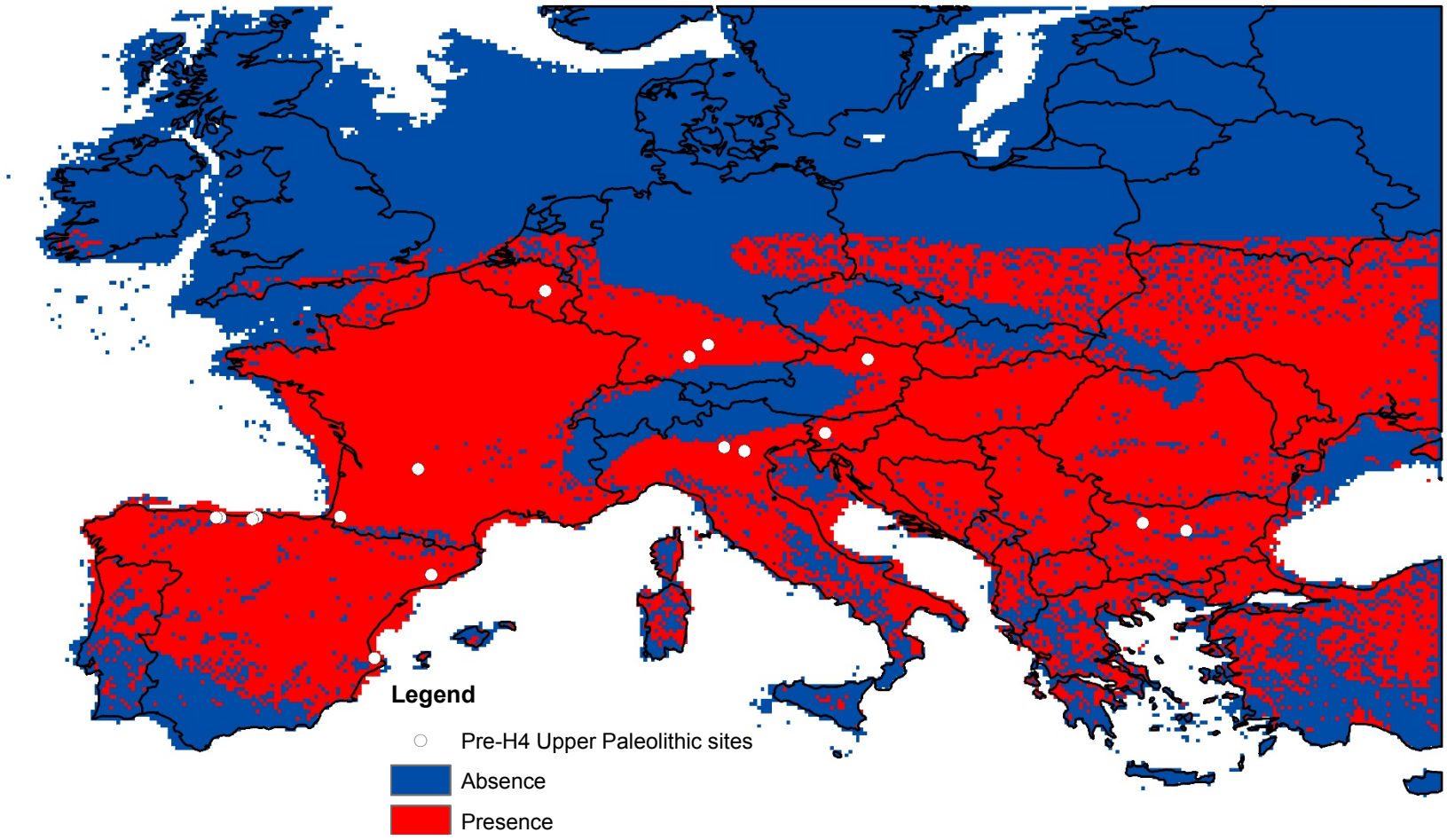

Figure 26. Maximum consensus prediction map for the Pre-H4 Upper Paleolithic exclusive model.

6.2 H4 (40.2 – 38.6 ky cal BP) Predictive Models

Five sets of consensus predictive models were generated for the H4 paleoenvironmental reconstruction, dated to 40.2 – 38.6 ky cal BP (Banks et al. 2008b) are described in Section 6.3: the Middle Paleolithic exclusive, technocomplex to fossil, Neandertal exclusive, Neandertal/Middle Paleolithic combined, and Upper Paleolithic exclusive. The time period of the H4 was characterized by large-scale climatic fluctuations and an overall much colder climate than the preceding Pre-H4 (Banks et al. 2008b; Daura et al. 2013; Huijzer and Isarin 1997).

6.2.1 Middle Paleolithic Exclusive Consensus Prediction Model

For the H4 paleoenvironmental reconstruction, the Middle Paleolithic exclusive sample consisted of 15 locations. The p-value for the consensus model was calculated with Pearson's P-value Compute (Pearson et al. 2007). Here $p = 0.001$ and the success rate was 62.5% for the consensus model (Table 26) upon which the majority, minimum, and maximum consensus prediction maps (Figures 27 – 29) are based. The probability value indicates that this model predicts known test points at a better than random rate and it is highly unlikely that these results are due to random chance. Thus, the null hypothesis of randomness was rejected.

In the majority prediction map (Figure 27), the pixels classified as present fall between latitudes of 49 and 36 degrees. Areas predicted present, and thus indicate the presence of suitable habitat, include the majority of the Iberian Peninsula, central and southern France, the Apennine Peninsula, the Balkan Peninsula, Anatolia, and the

islands of Ibiza, Palma, Menorca, Corsica, Sardinia, and Sicily. A few scattered areas north of the Alps in Belgium, Luxemburg, Germany, Austria, and the Czech Republic were classified as present as well. Large portions of the Dinaric Alps, Balkan Mountains, and Carpathian Mountains were also predicted as showing suitable habitat. The prediction closely follows the present-day shoreline despite the lower sea-levels of the time. Twenty-nine percent of the total study area (16,938 pixels) is predicted as present (Table 27), a decrease of 8% from the Middle Paleolithic exclusive model during the Pre-H4.

The minimum consensus prediction map (Figure 28) classifies only 4,837 pixels as present (0.08 total study area) (Table 27). The pixels are slightly more constricted latitudinally when compared to the majority consensus prediction map and fall between 48.5 and 36.75 degrees. In the most conservative interpretation of this model, the areas of suitable habitat are found on the Iberian Peninsula, the Balearic Islands of Mallorca and Menorca, central and southern France, Sardinia, the Apennine Peninsula including the Po River Valley, and scattered across the Great Hungarian Plain, the Balkan Peninsula, the Dnieper Uplands, and a small portion of northern and central Anatolia. The Iberian Peninsula shows the most concentration of areas predicted present in the minimum model and nearly the entirety of the Ebro River Valley is highlighted in red, along with portions of the Meseta Central. The areas of Iberia not predicted as showing suitable habitat are the southern extremes of the Peninsula and portions of the Meseta Central.

The maximum consensus prediction map (Figure 29) designates 25,978 pixels as present (45% of the total study area) (Table 27). The least conservative map of the model shows the least amount of latitudinal constriction, with suitable habitat falling between 51.5 and 36 degrees. The area predicted present is the most continuous of the three maps reported here, with only the Alps and southern tip of Iberia showing as an area of absence.

P	0.001
Success rate	0.625

Table 26. Validation for H4 Middle Paleolithic exclusive model with Pearson's P-value Compute.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	16,938	41,313	0.29
Minimum	4,837	53,414	0.08
Maximum	25,978	32,273	0.45

Table 27. Pixel ratios for the H4 Middle Paleolithic exclusive prediction maps.

The majority, minimum, and maximum consensus prediction maps for the Middle Paleolithic exclusive sample during the H4 being on the following page.

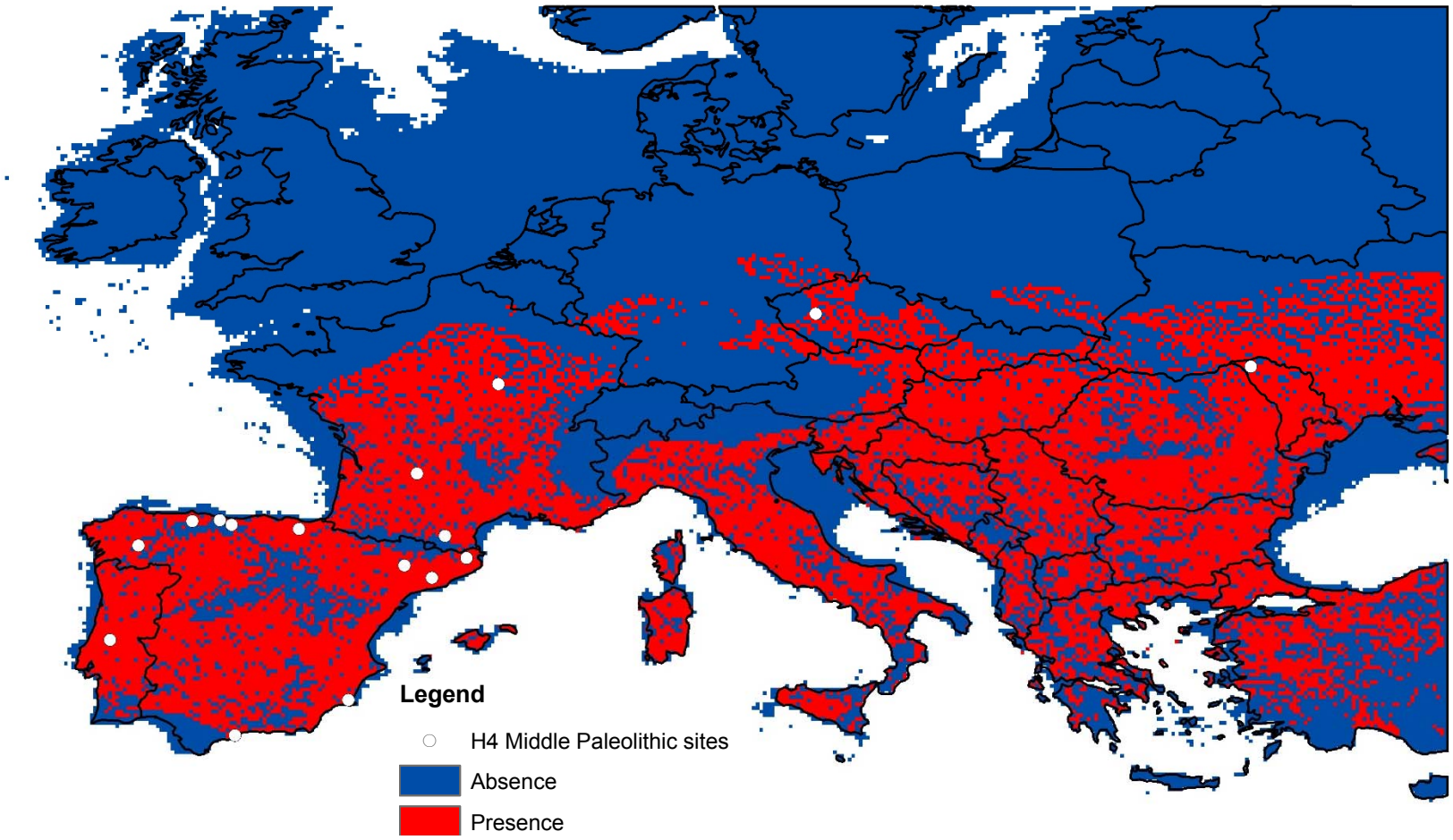

Figure 27. Majority consensus prediction map for H4 Middle Paleolithic exclusive model.

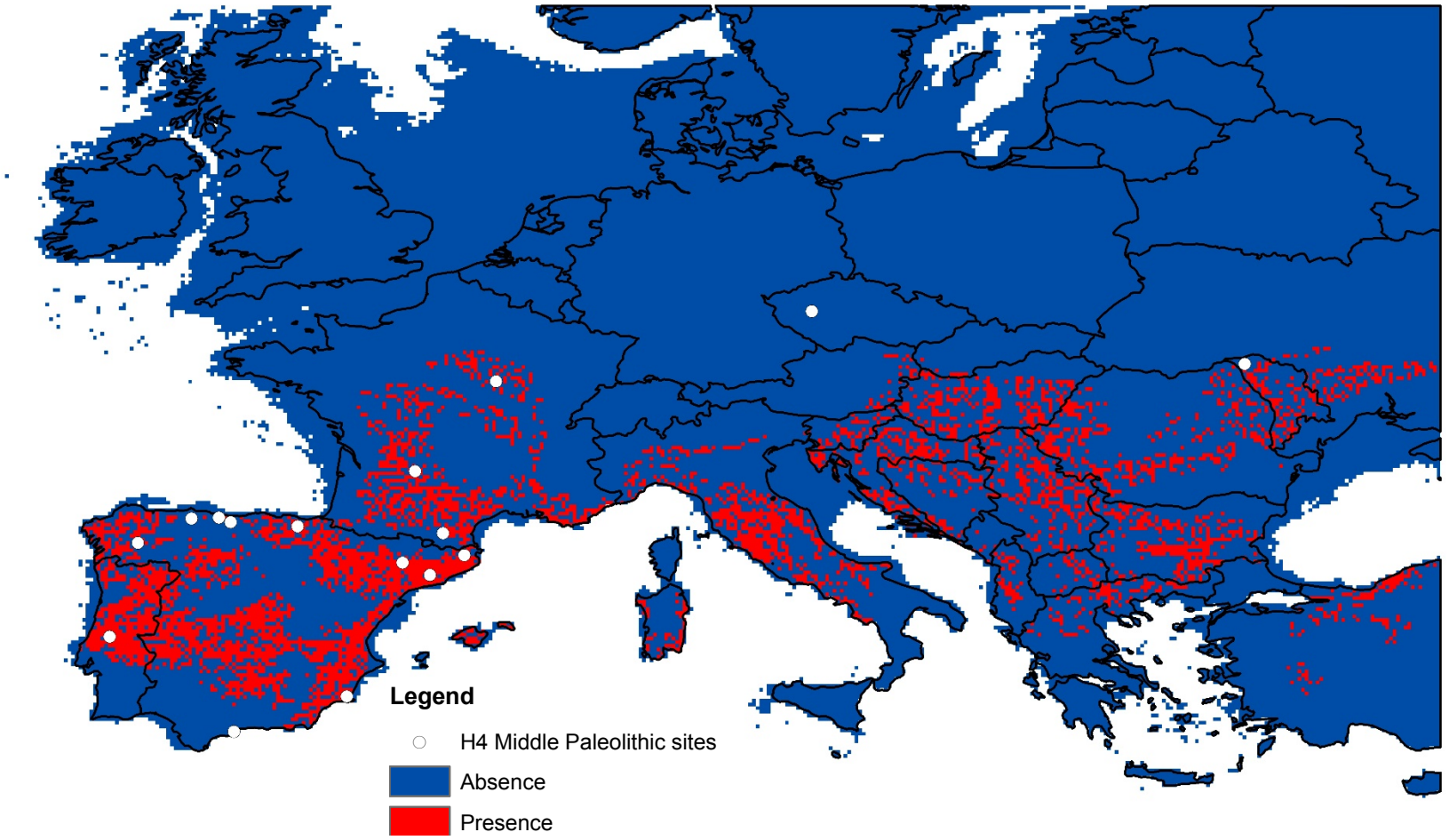

Figure 28. Minimum consensus prediction map for H4 Middle Paleolithic exclusive model.

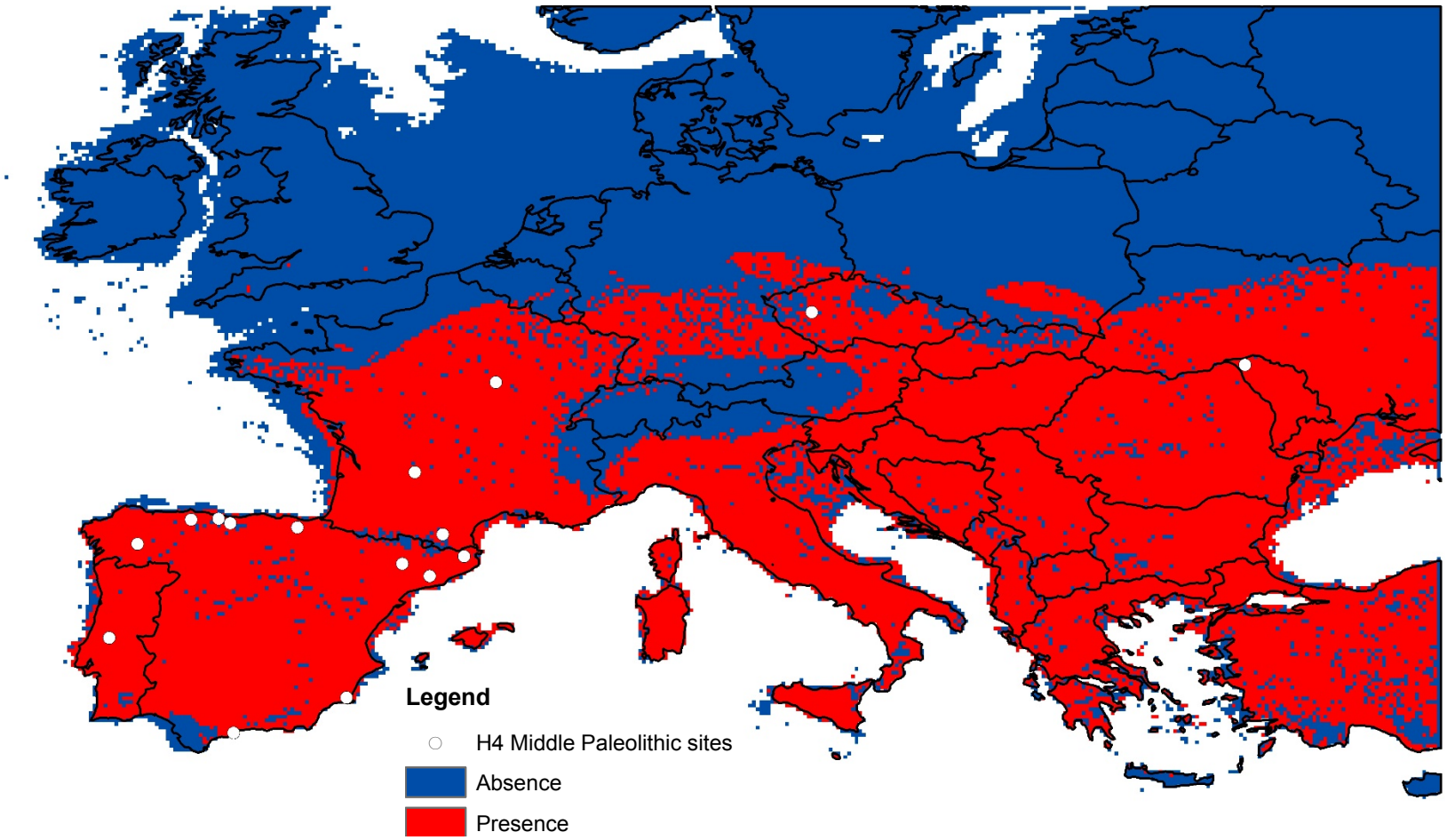

Figure 29. Maximum consensus prediction map for H4 Middle Paleolithic exclusive model.

6.2.2 Technocomplex to Fossil Consensus Prediction Model

This consensus prediction model was calibrated with a sample of 15 Middle Paleolithic archaeological sites at which no diagnostic hominin remains have been found dating to the H4. It was tested on its ability to correctly classify a sample of 6 Neandertal fossil locations dating to the same period. After thresholding, the model had a success rate of 83%, where 5 out of 6 test points were correctly classified as present. The test point that was not correctly identified by the model was the Gibraltar site complex. Pearson's P-value Compute (Pearson et al. 2007) was used to generate the consensus p-value for the thresholded model, here $p = 0.003185$ (Table 28). This value indicates that the model created with H4 Middle Paleolithic sites was able to predict known locations with Neandertal remains at a better than random rate and the null hypothesis can be rejected.

Even though the sea level of this paleoenvironmental reconstruction is 90 m lower than present day, the thresholded prediction (Figure 30) largely follows modern shorelines except for a few scattered areas on the Adriatic and Black Sea shelves. The majority of the Iberian Peninsula shows the presence of suitable habitat based on the Middle Paleolithic archaeological sites from the H4. No pixels north of 52 degrees latitude are predicted as present. It should be noted that this thresholded prediction is very similar in scope to the maximum prediction for the Middle Paleolithic exclusive model for the H4. Suitable habitat was also identified in most of present-day France, Ibiza, Mallorca, Menorca, Sardinia, Corsica, Sicily, the Apennine Peninsula, central and southern Germany, the Great Hungarian Plain, the Balkan Peninsula, the majority of the

area surrounding the Carpathian Mountains, and Anatolia. A few scattered pixels of suitable habitat were also identified in southern England. The Alps and Pyrenees Mountains appear as areas where suitable habitat is not present, but the Dinaric Alps, Balkan Mountains, and Carpathian Mountains show greater inclusion of predicted presence within their borders.

The Partial-ROC score was calculated for the un-thresholded prediction (Figure 31). The probability (*P*) that the mean is ≤ 1.0 is very slight and is significantly elevated above random expectations. The resulting probability value equals $8.4x10^{-8}$ (Table 29). Thirty-four percent of the total study area (19,883 pixels) was never predicted as present by any of the 10 best subsets models. All ten best subsets were in agreement on 16,375 pixels as present (28% of the total study area).

P	0.003
Critical Binomial Value	4
Test points correctly classified as present	5
Success rate	0.83

Table 28. Cumulative binomial probability results for the thresholded H4 technocomplex to fossil model.

Minimum	1.35
Maximum	1.72
Mean	1.62
SD	0.12
Replicates ≤ 1	0
Z-statistic	165.44
P	$8.40x10^{-8}$

Table 29. Partial-Roc validation results for the H4 technocomplex to fossil model.

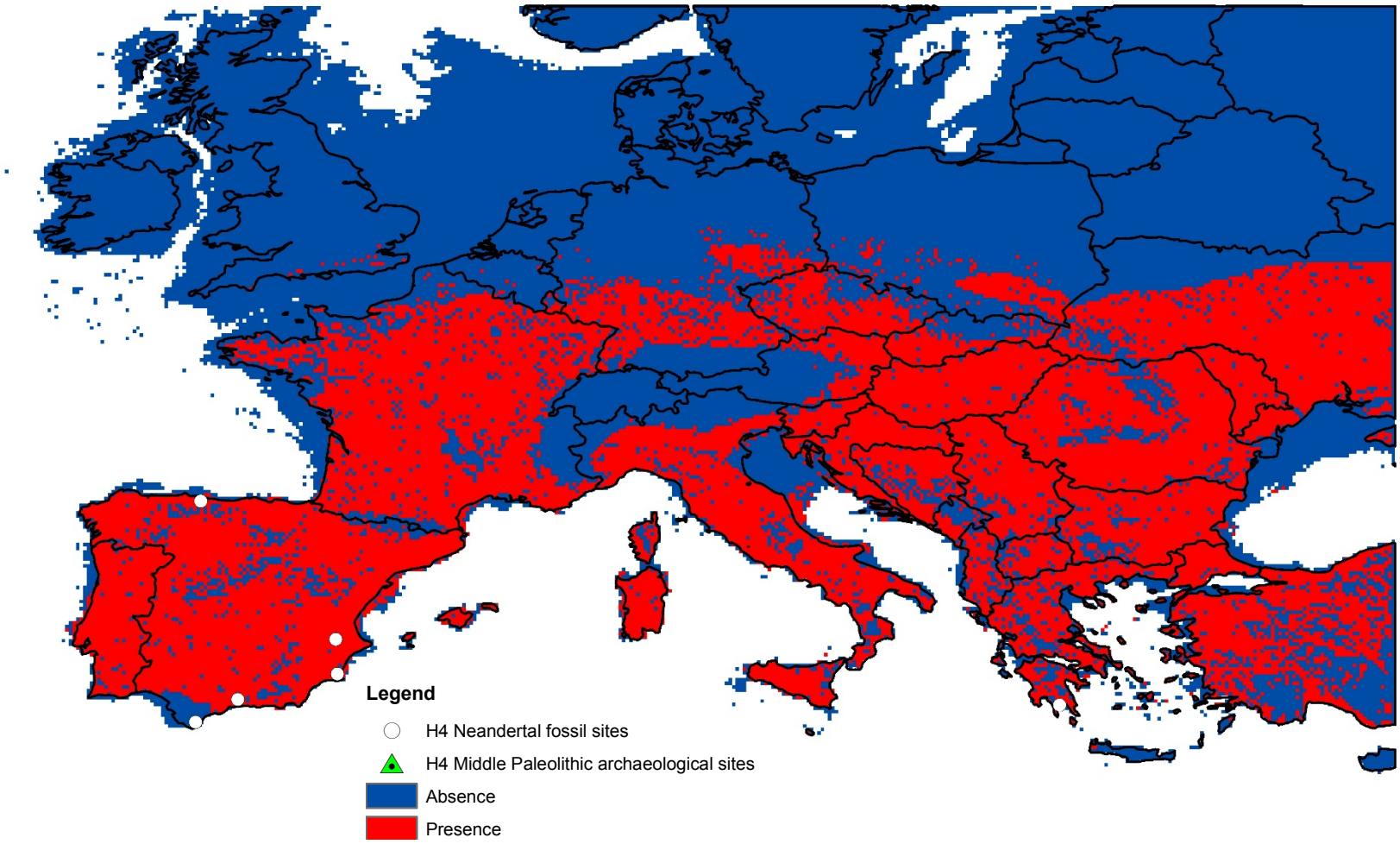

Figure 30. Thresholded consensus prediction map for the technocomplex to fossil model, generated with Middle Paleolithic archaeological sites (*n* = 15) and validated Neandertal fossil locations (*n* = 6) for the H4.

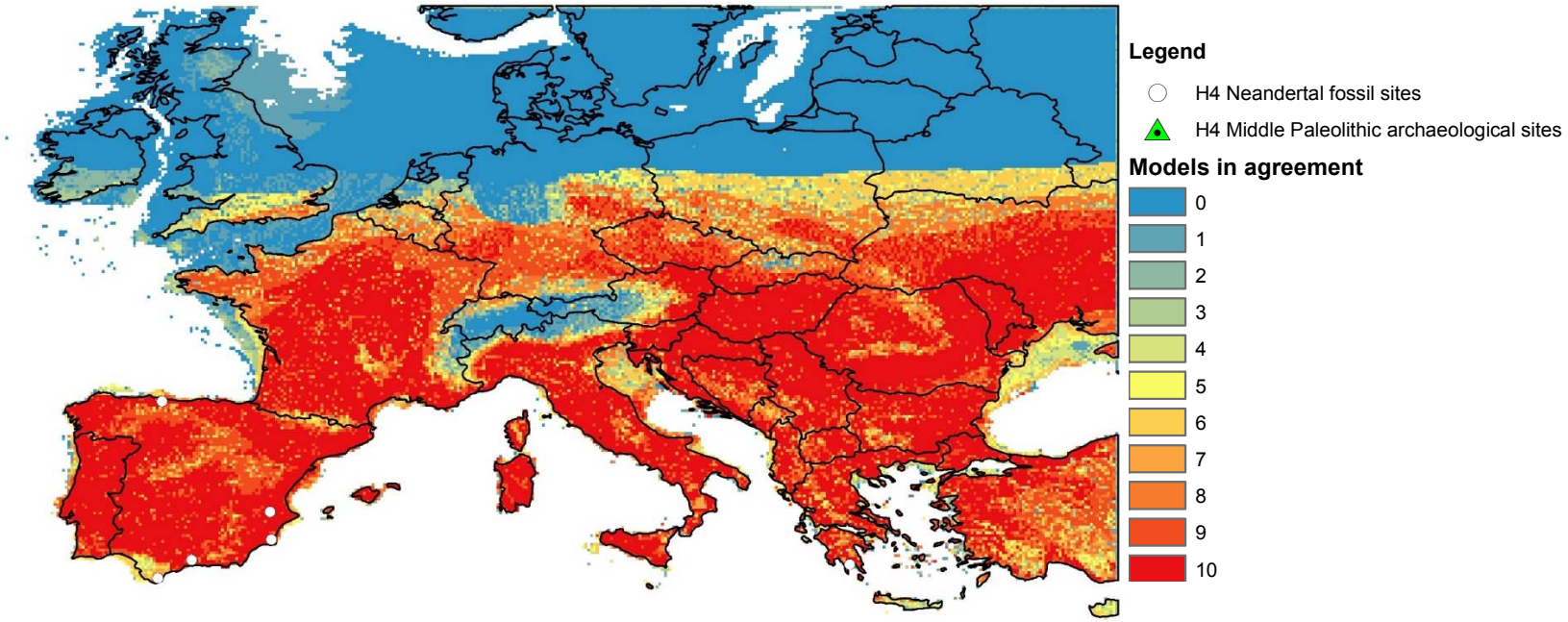

Figure 31. Unthresholded consensus prediction map for the technocomplex to fossil model, generated with Middle Paleolithic archaeological sites (*n* = 15) and validated Neandertal fossil locations (*n* = 6) for the H4.

6.2.3 Neandertal Exclusive Model

The number of sites with Neandertal remains dated to the H4 (n = 6) drops drastically from the previous Pre-H4 period (n = 13). Even though a sample size of 6 is smaller than is typically used in ecological research, this project sought to run an experiment with the limited number of H4 Neandertal fossil locations to determine if a statistically accurate model could be generated from the available data. The p-value was 0.02 and success rate was 33% (2 out of 6 test points correctly classified) (Table 30).

While the p-value is significant, the success rate of this model in correctly classifying omitted test points is less than is usually considered good. Experiments with GARP at such extremely small sample sizes have also been shown to be less than ideal (Pearson et al. 2007) and when compared to the results for the Pre-H4 Neandertal exclusive model, the following results are limited in their geographic prediction.

The areas predicted as present are more geographically restricted than seen in any of the previous models created for this project. The presence prediction is restricted to the southern-most portions of Europe. On the majority consensus prediction map (Figure 32), the highest concentration is located in the southern Iberian Peninsula, beneath the Sistema Iberico Mountains and Meseta Central uplands. There are a few pixels predicted present by some of the replicates in the Ebro River Valley, but the majority are concentrated in the southwestern lowlands and along the eastern coast of the peninsula. The areas predicted present also tend to appear patchy and discontinuous. Only 4% of the study area was classified as present in the majority consensus prediction map (2,403 pixels) (Table 31).

The minimum consensus prediction map (Figure 33) classifies only 376, less than 1% of the study area, of pixels as present (Table 31). This is an enormous restriction when compared to all previous models generated by this study. The small areas where all the thresholded best-subset runs were in agreement are found only along the eastern coast of Spain, scattered in southwestern Iberia, Ibiza, Mallorca, Corsica, Sardinia, Sicily, central and southern Italy, the Balkan Peninsula, and western Turkey. It is possible that this extreme geographic restriction of associated environmental variables could be due, in part, to the small sample size used to calibrate the model.

The area classified as present by the maximum consensus prediction map (Figure 34) rises to 19% of the total study area (10,787 pixels), an area 18.4% greater than was seen with the minimum consensus prediction map and 15% greater than the majority consensus prediction map (Table 31). This least conservative model, where a pixel was designated present if any of the thresholded best-subset runs classified it as such, is the first that classified large areas of the Adriatic and Black Sea shelves as present. In addition, there was an area predicted as present along the coast of present-day Scotland and England and under the North Sea which was not seen in any previous models. The main areas predicted present on this map area more latitudinally constrained in the western portion of the map than they are on the east, if the isolated area predicted present in the North Sea is not included in the main body of suitable habitat identified by the maximum map. The overall nature of the prediction is quite discontinuous with isolated pixels predicted present appearing in many portions of the study area. The main concentrations of continuous predictions are concentrated in the southwestern corner of

Iberia, along the eastern coast of the Iberian Peninsula, the eastern coast of the Apennine Peninsula, the Adriatic shelf, and the Black Sea shelf.

P	0.02
Success rate	0.33

Table 30. Validation for the H4 Neandertal exclusive model.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	2,403	55,848	0.04
Minimum	376	57,875	0.006
Maximum	10,787	47,464	0.19

Table 31. Pixel ratios for the H4 Neandertal exclusive predictions.

The majority, minimum, and maximum consensus prediction maps for the H4 Neandertal consensus model begin on the following page (Figures 32 – 34).

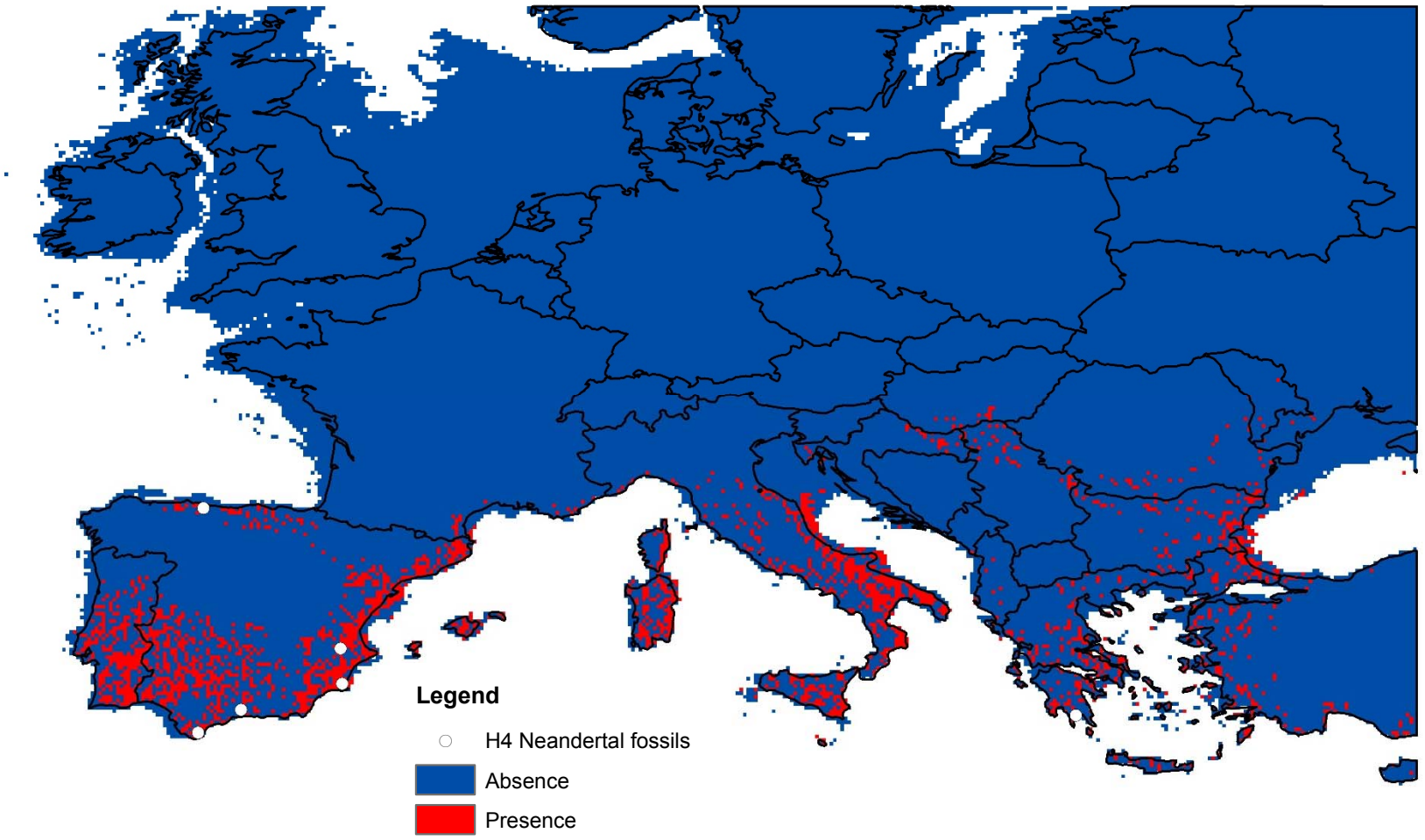

Figure 32. Majority consensus prediction map for the H4 Neandertal internal model.

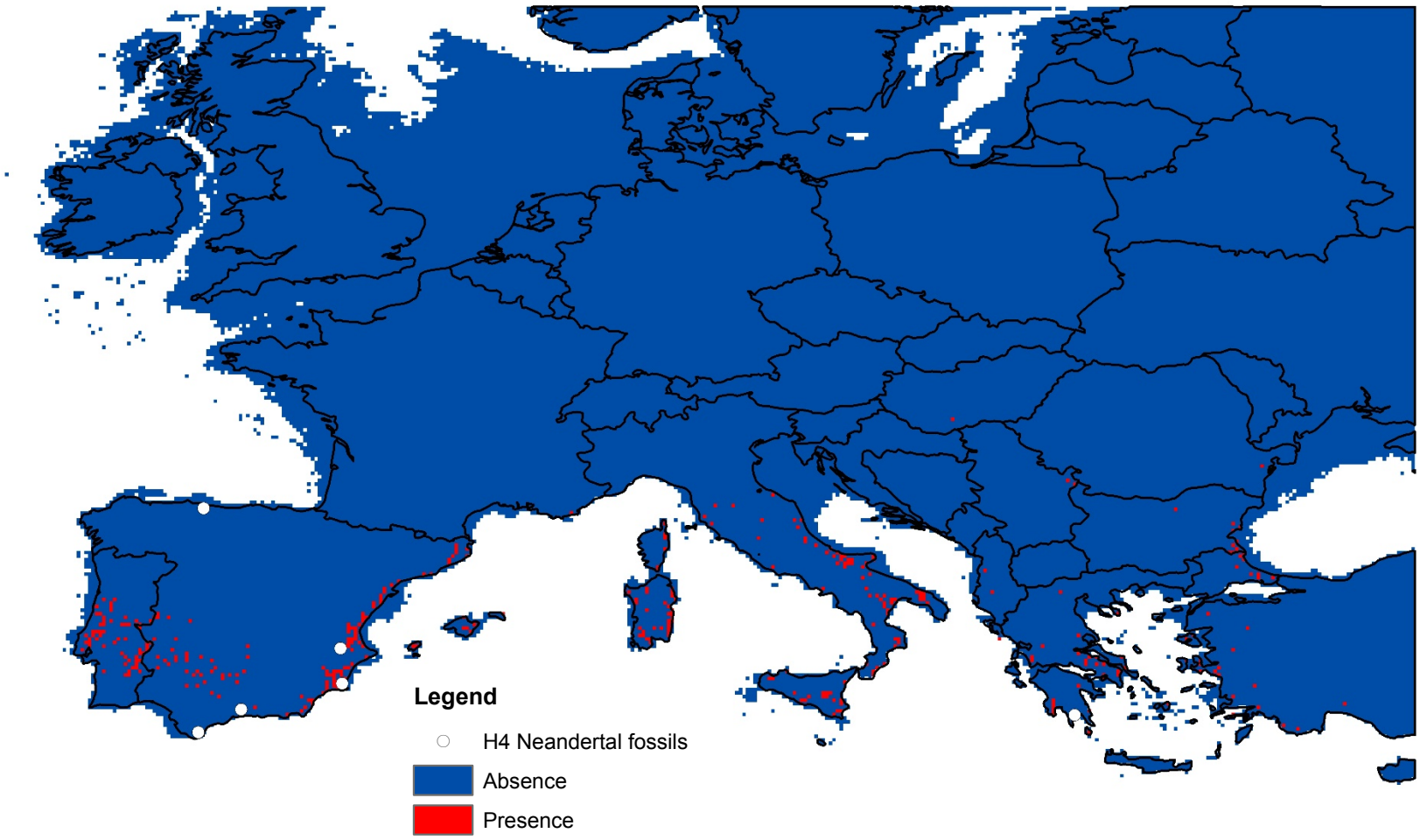

Figure 33. Minimum consensus prediction map for the H4 Neandertal internal model.

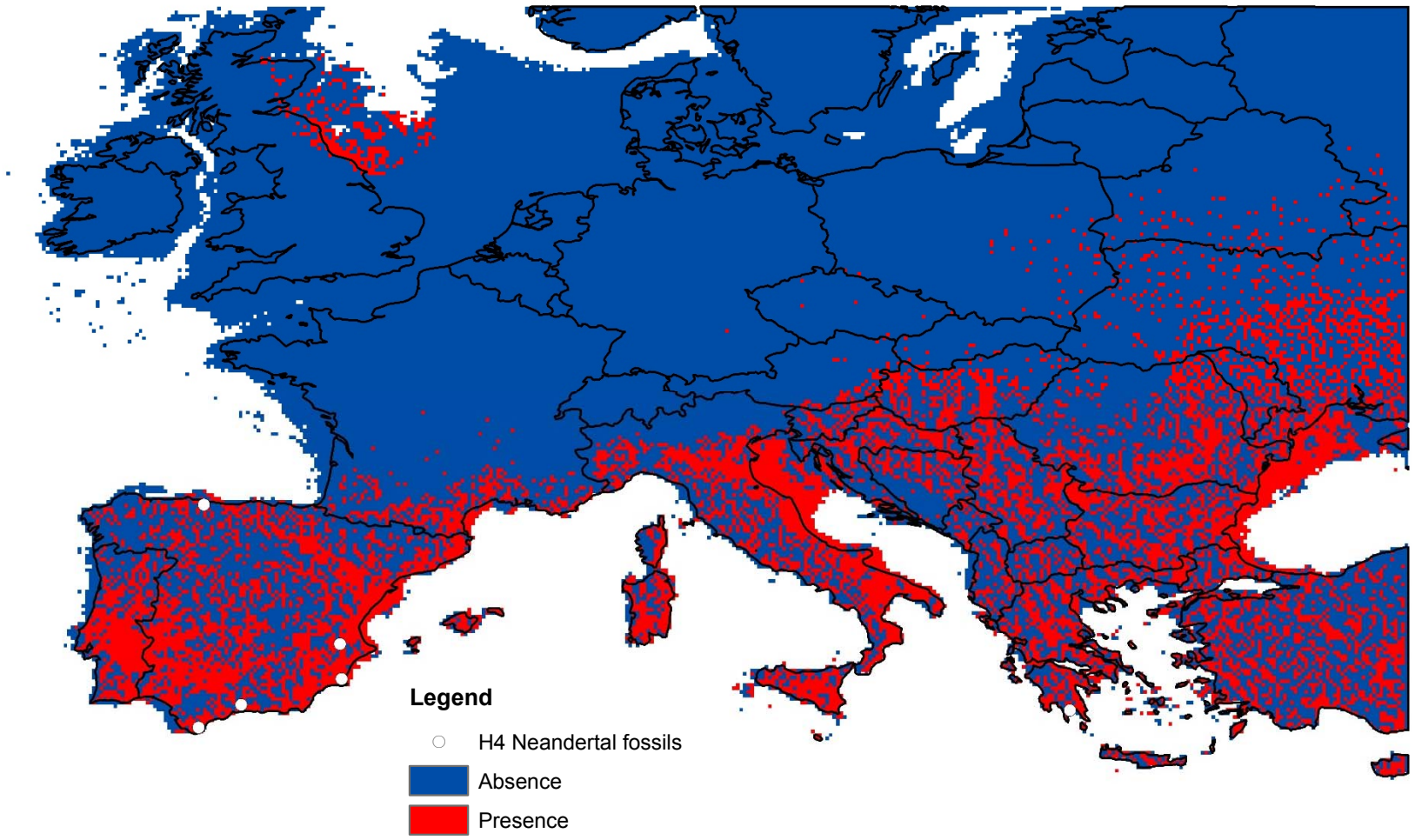

Figure 34. Maximum consensus prediction map for the H4 Neandertal internal model.

6.2.4 Neandertal Fossil and Middle Paleolithic Archaeological Combined Sample

The sample size for the Neandertal/Middle Paleolithic combined H4 experiment jumps to 21 presence points when compared to the Neandertal exclusive sample from the same period. This increase gives ecological niche modeling (ENM) algorithms such as GARP a much better chance of creating good predictive models. With the randomization and splitting/sorting experimental design described in Section 5.3.2, all *p*-values generated with cumulative binomial probabilities were ≤ 0.02 (Table 32) and all Partial-ROC scores were ≤ 0.02 (Table 33) as well. All 5 replicate runs met or exceeded the critical binomial values required for those runs to meet statistical significance.

The above values indicate that this model predicts known test points at a better than random rate and the null hypothesis that these results are due to random chance is rejected. While the *p*-values for the Neandertal/Middle Paleolithic combined and Neandertal exclusive experiments during the H4 are identical, the Neandertal/Middle Paleolithic combined results fare extremely well with the higher power statistical tests used here and each of the replicate runs predicted a greater total number of known test points than the H4 Neandertal exclusive.

The areas indicating suitable habitat (those predicted present) on the majority consensus prediction map (Figure 35) are largely confined to southern Europe, below 49.7 degrees North latitude and south of the Carpathian Mountains. No areas north of the Alps are predicted present. Geographic areas where the majority of thresholded best-subsets replicates predict similar suitable habitat include the majority of the Apennine Peninsula, the Great Hungarian Plain, the Balkan Peninsula, the western portion of the

Anatolian Peninsula, the Dnieper Uplands, the lowlands directly south of the Carpathian Mountains, southern France, and the majority of the Iberian Peninsula. On the Iberian Peninsula, the Ebro River Valley and the southern extent of the peninsula show extensive areas of suitable habitat. The islands of Ibiza, Menorca, Mallorca, Sardinia, Corsica, and Sicily are largely included in the prediction. Twenty percent of the study area is classified as present (11,671 pixels) (Table 34).

In contrast, the much more conservative minimum consensus prediction map (Figure 36) for this model only classifies 6% of the total study area as present for suitable habitat (3,249 pixels) (Table 34). The geographic areas predicted present are further restricted from the majority map to fall south of 46.3 degrees latitude. Suitable habitat is present in the southern Iberian Peninsula, the Ebro River Valley, along the eastern coast of Spain, the southern coast of France, the Apennine Peninsula, scattered along the Danube River Valley south of the Carpathian Mountains, the southern portions of the Balkan Peninsula, the western Anatolian Peninsula, and the major Mediterranean islands (except Crete).

The maximum consensus prediction map (Figure 37) for the H4 Neandertal/Middle Paleolithic combined sample reaches only slightly farther north than was seen in the majority map, with the northernmost pixels predicted present at 50.3 degrees. Even though this is the least conservative map illustrating this predictive model, Neandertal suitable habitat is restricted much farther south than was seen during the Pre-H4. The only new areas predicted present on this map include central France. No area

north of the Alps was predicted as present. The maximum area of suitable habitat is 32% of the study area, or 18,787 pixels classified as present (Table 34).

Evaluation replicates	Cumulative binomial values	Critical binomial values	Success ratios
Evaluation set 1	0.01	5	0.50
Evaluation set 2	0.007	4	0.50
Evaluation set 3	0.001	4	0.60
Evaluation set 4	0.01	5	0.50
Evaluation set 5	0.02	3	0.30

Table 32. Results of the statistical validation procedures using cumulative binomial probabilities and critical binomial values for the Neandertal/Middle Paleolithic combined sample during the H4.

	1	**2**	**3**	**4**	**5**
Minimum	1.32	0.84	1.42	1.32	0.89
Maximum	1.77	1.80	1.78	1.76	1.89
Mean	1.59	1.43	1.62	1.54	1.50
SD	0.09	0.20	0.09	0.09	0.19
Replicates ≤ 1	0	30	0	0	9
Z-statistic	205.54	67.26	214.79	172.56	81.40
P	4.02×10^{-11}	0.02	5.5×10^{-12}	1.69×10^{-8}	0.005

Table 33. Results of the Partial-ROC analysis for the Neandertal/Middle Paleolithic combined consensus model during the H4.

	Pixels predicted present	Pixels predicted absent	Ratio of present/total
Majority	11,671	46,580	0.20
Minimum	3,249	55,002	0.06
Maximum	18,787	39,464	0.32

Table 34. Pixel counts and ratios from the majority, minimum, and maximum consensus prediction maps for the Neandertal/Middle Paleolithic combined model for the H4.

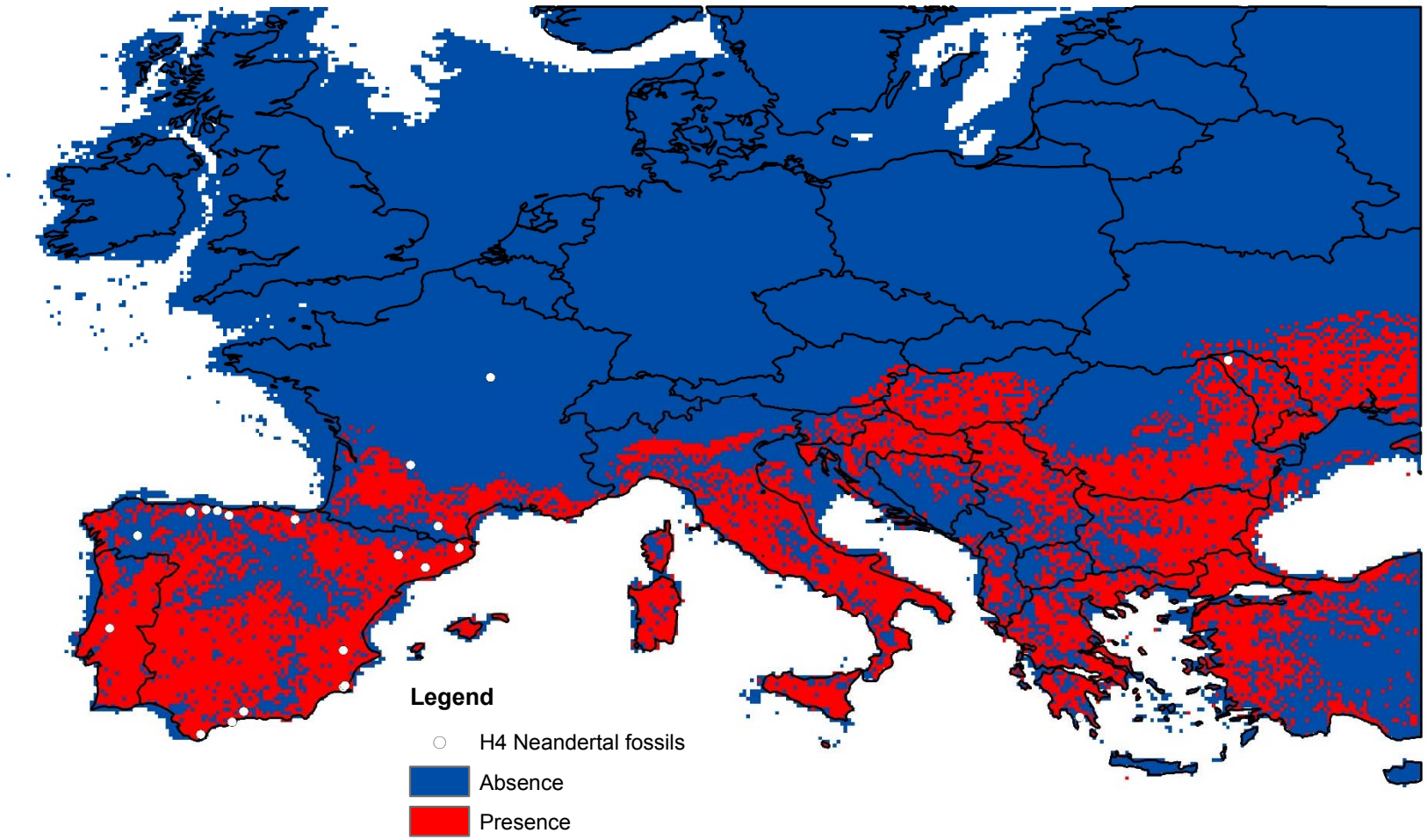

Figure 35. Majority consensus prediction map for the combined sample of Neandertal fossil locations (*n* = 14) and Middle Paleolithic archaeological sites that have not produced diagnostic hominin remains (*n* = 23) for the H4.

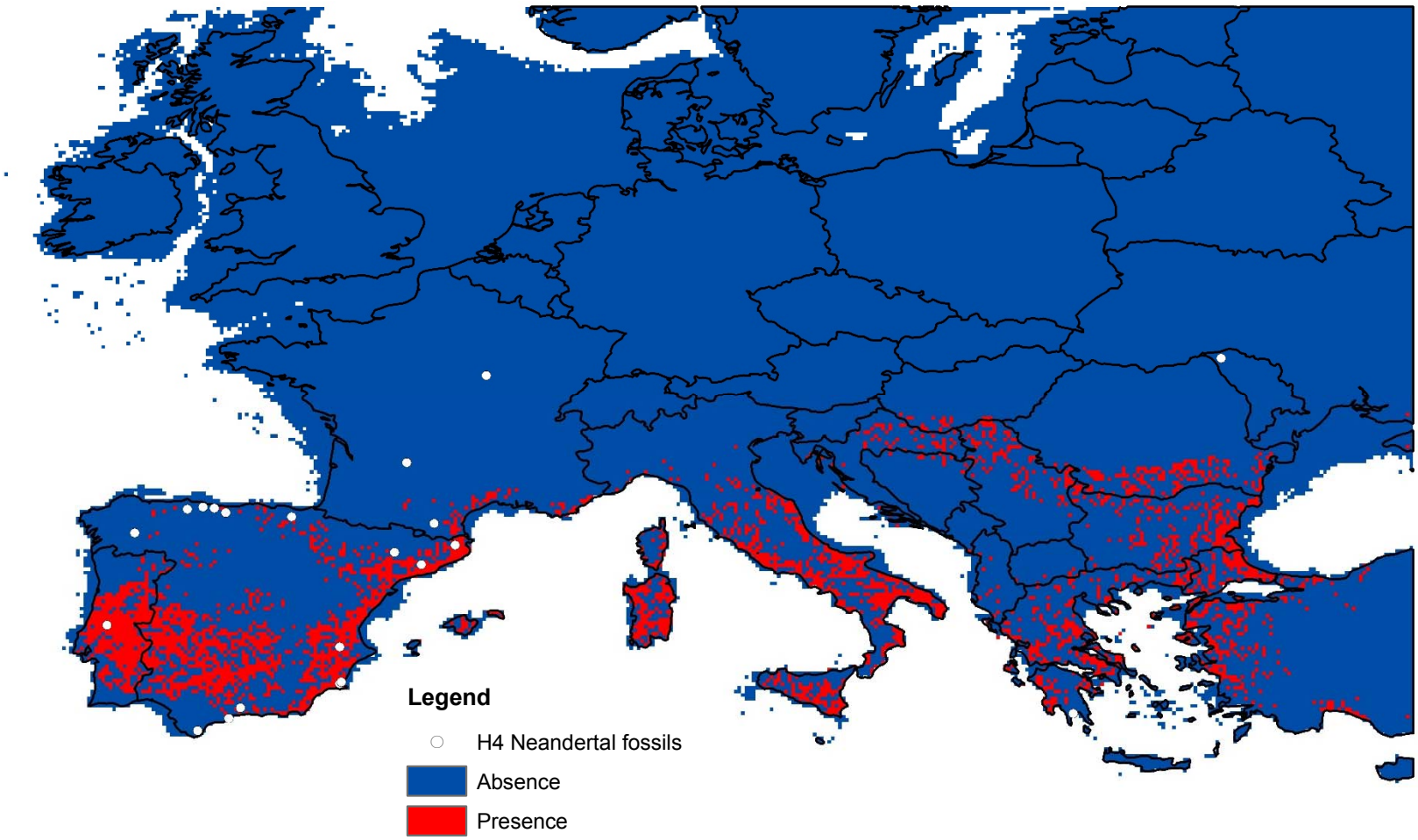

Figure 36. Minimum consensus prediction map for the combined sample of Neandertal fossil locations (*n* = 14) and Middle Paleolithic archaeological sites that have not produced diagnostic hominin remains (*n* = 23) for the H4.

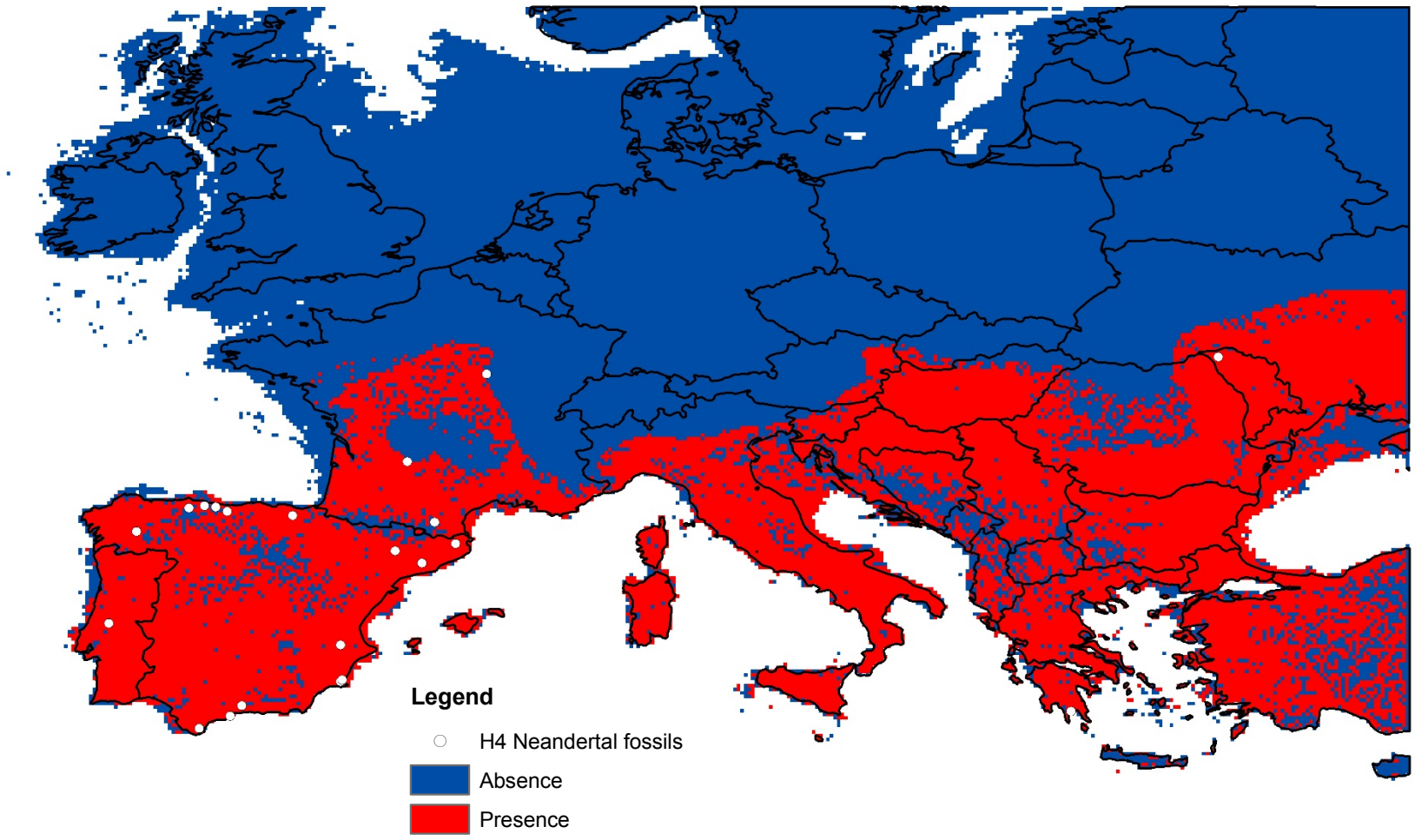

Figure 37. Maximum consensus prediction map for the combined sample of Neandertal fossil locations (*n* = 14) and Middle Paleolithic archaeological sites that have not produced diagnostic hominin remains (*n* = 23) for the H4.

6.2.5 Upper Paleolithic Exclusive Consensus Prediction Model

The following consensus prediction model for the H4 paleoenvironmental reconstruction was generated with a sample of Upper Paleolithic archaeological sites absolutely dated ($n = 24$). Based on cumulative binomial values, all p-values were $\leq$ 0.03 (Table 35). All Partial-ROC scores calculated for each of the 5 random replicate runs were ≤ 0.01 (Table 36). Thus, it can be concluded that all results were significantly elevated over random expectations and the null hypothesis of obtaining these results via randomness can be rejected.

The majority consensus prediction map (Figure 38) classifies 24% of the study area as present (14,270 pixels) (Table 37). Areas of suitable habitat where at least 3 of the 5 replicate runs agree on a presence prediction include the majority of France, areas north of the Alps, extensive areas on the Great Hungarian Plain, the Dnieper Uplands, the Balkan Peninsula, the Apennine Peninsula, the Anatolian Peninsula, and the Iberian Peninsula. The areas on the majority prediction map for the Upper Paleolithic exclusive sample are not as latitudinally constricted as the majority maps for the previous models created for the H4 to model Neandertal presence. On the Iberian Peninsula specifically, the Ebro River Valley is a concentrated geographic area of predicted suitable habitat. Pixels falling well south of the hypothesized Ebro Frontier are also shown to have suitable habitat for the makers of the Upper Paleolithic, the early modern humans (EMHs).

The minimum consensus prediction map (Figure 39), where all 5 thresholded replicate runs agree on the geographic location of suitable habitat, predicts 10% of the

study area as present (5,888 pixels) (Table 37). While this total area predicted present for this minimum map and the minimum map for the Neandertal/Middle Paleolithic combined model for the H4 only varies by 4%, the geographic distribution of those areas is vastly different. The Upper Paleolithic exclusive minimum prediction map shows areas of high habitat suitability much farther north than is shown for Neandertals, falling between 49.6 and 37.8 degrees. These areas include large portions of France, the head of the Po River Valley, the western portion of the Great Hungarian Plain, the lowlands surrounding the Southern Carpathian Mountains, the northwest corner of the Iberian Peninsula, the Ebro River Valley, and scattered pixels throughout central Iberia.

The maximum consensus prediction map (Figure 40) is the least conservative illustration of the model described here for the Upper Paleolithic exclusive sample during the H4, and that is reflected in the latitudinal extent of the areas predicted by one or more of the 5 replicate runs as present. All pixels classified as present fall between 53 and 35.1 degrees N. A total of 23,000 pixels were predicted present, or 39% of the total study area (Table 37). The areas predicted present here appear much more contiguous than was seen in the majority and minimum consensus prediction maps, except for the areas north of the predicted presence seen on the majority map. Much larger areas of central and southern Iberia are included on this map as present, along with some scattered pixels in southern Ireland and along the southern coast of England. Larger areas of the Adriatic and Black Sea shelves are predicted present and Crete is also designated as such. The Alps are a distinct area of absence on this map. The Pyrenees, Dinaric Alps, Carpathian Mountains, and the Balkan Mountains include larger scattered

areas predicted present on the maximum consensus prediction map. Only a few scattered pixels are predicted as present in the English Channel.

Evaluation replicates	P-value	Critical Binomial Value	Success rate
Evaluation set 1	1.49559×10^{-4}	5	0.66
Evaluation set 2	0.005003189	6	0.58
Evaluation set 3	0.030348687	6	0.5
Evaluation set 4	7.6281×10^{-5}	5	0.66
Evaluation set 5	0.007286397	5	0.5

Table 35. Validation for thresholded predictions, H4 Upper Paleolithic exclusive model.

	1	2	3	4	5
Minimum	0.730281	1.259833	1.029180	1.188147	0.818944
Maximum	1.777367	1.727129	1.712872	1.794718	1.777299
Mean	1.453098	1.540004	1.385194	1.595147	1.455133
SD	0.20634	0.094434	0.140341	0.117574	0.173467
Replicates ≤ 1	28	0	0	0	8
Z-statistic	69.43993	180.83	86.79515	160.0714	82.9701
P	0.01405	5.38×10^{-9}	0.003028	2.08×10^{-7}	0.004348

Table 36. Partial-ROC scores for the H4 Upper Paleolithic exclusive models.

	Pixels predicted present	Pixels predicted absent	Ratio of present/total
Majority	14,270	43,981	0.24
Minimum	5,888	52,363	0.10
Maximum	23,000	35,251	0.39

Table 37. Pixel ratios for the H4 Upper Paleolithic exclusive predictions.

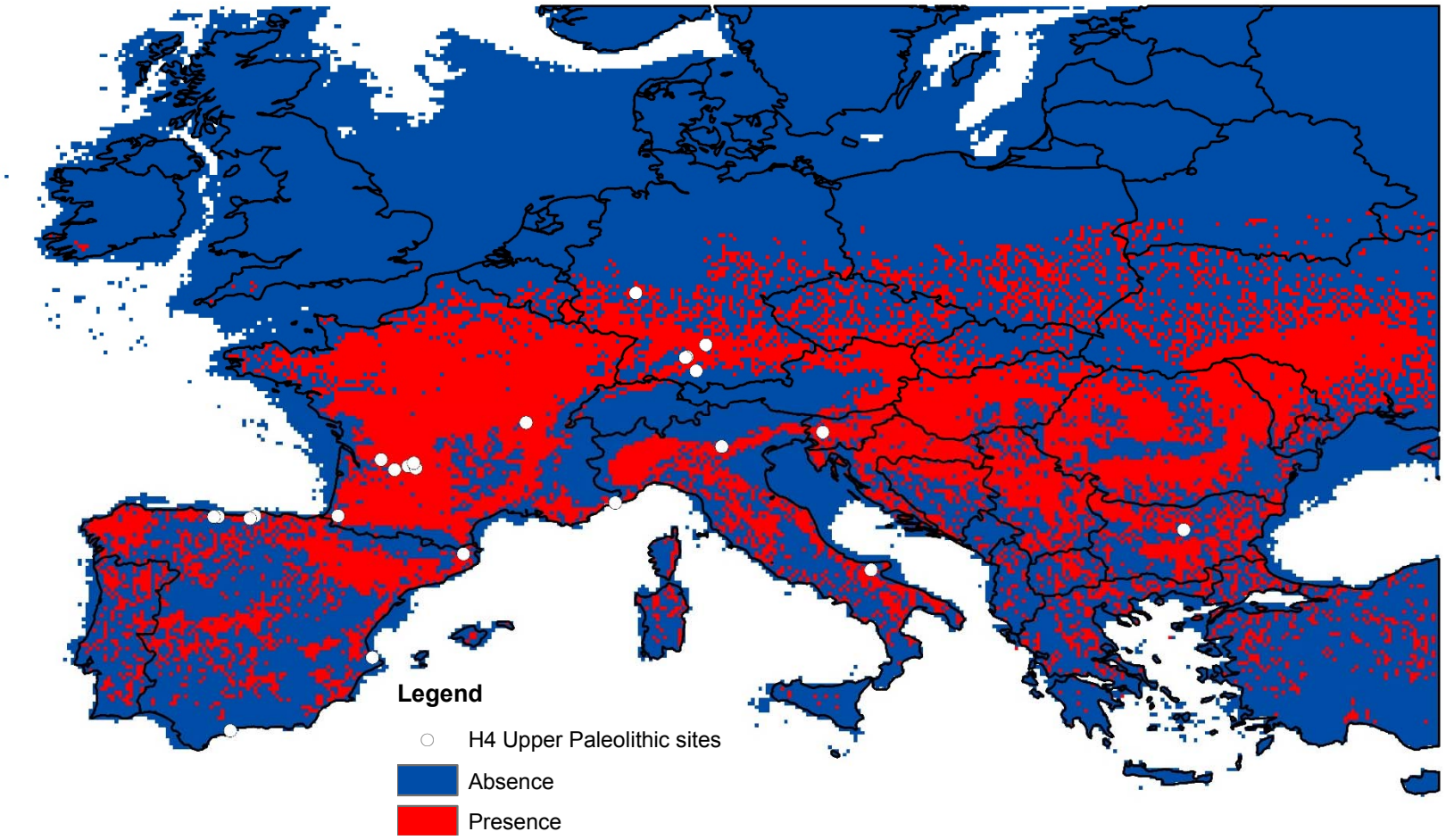

Figure 38. Majority consensus prediction map for the H4 Upper Paleolithic exclusive model.

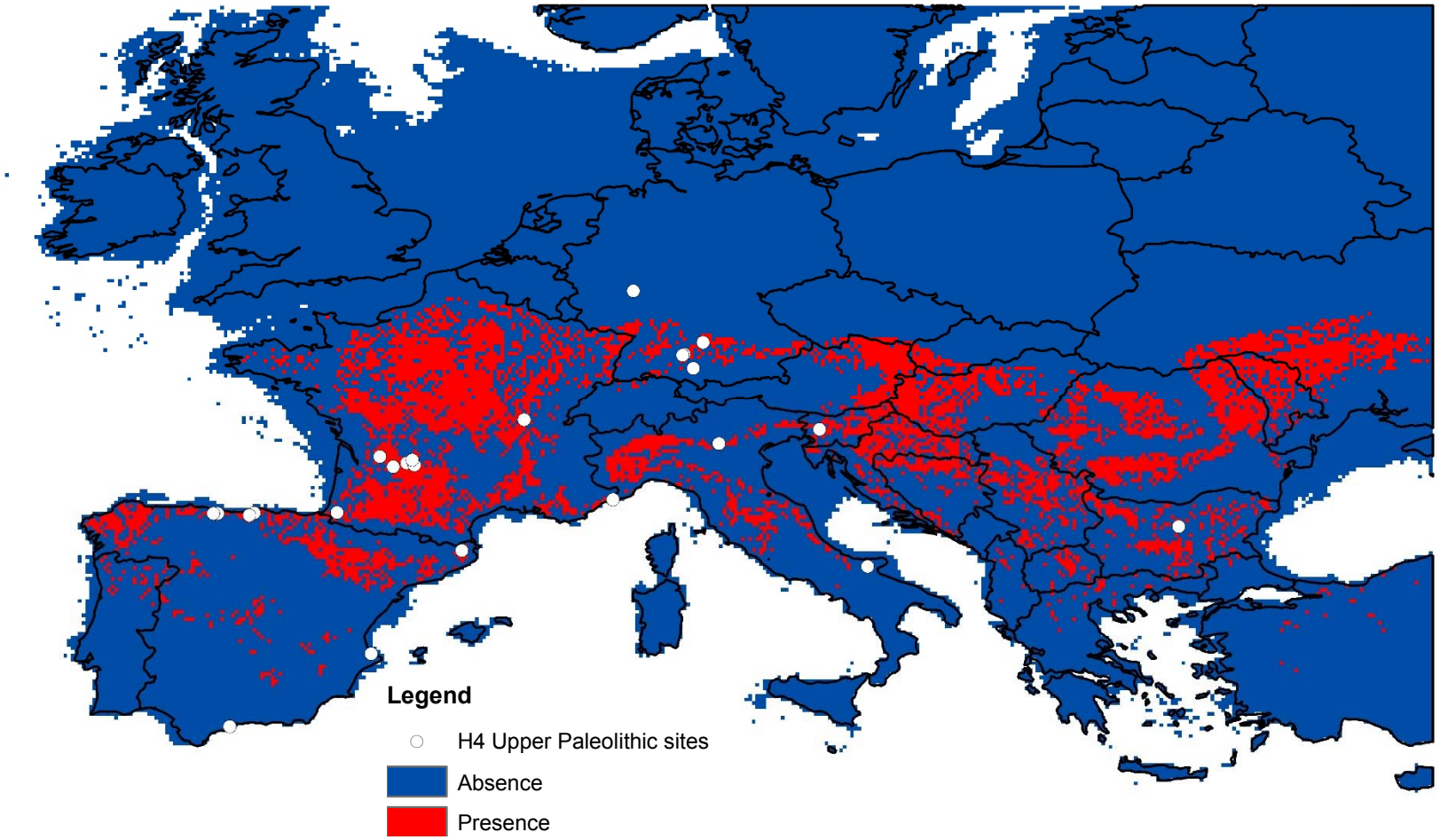

Figure 39. Minimum consensus prediction map for the H4 Upper Paleolithic exclusive model.

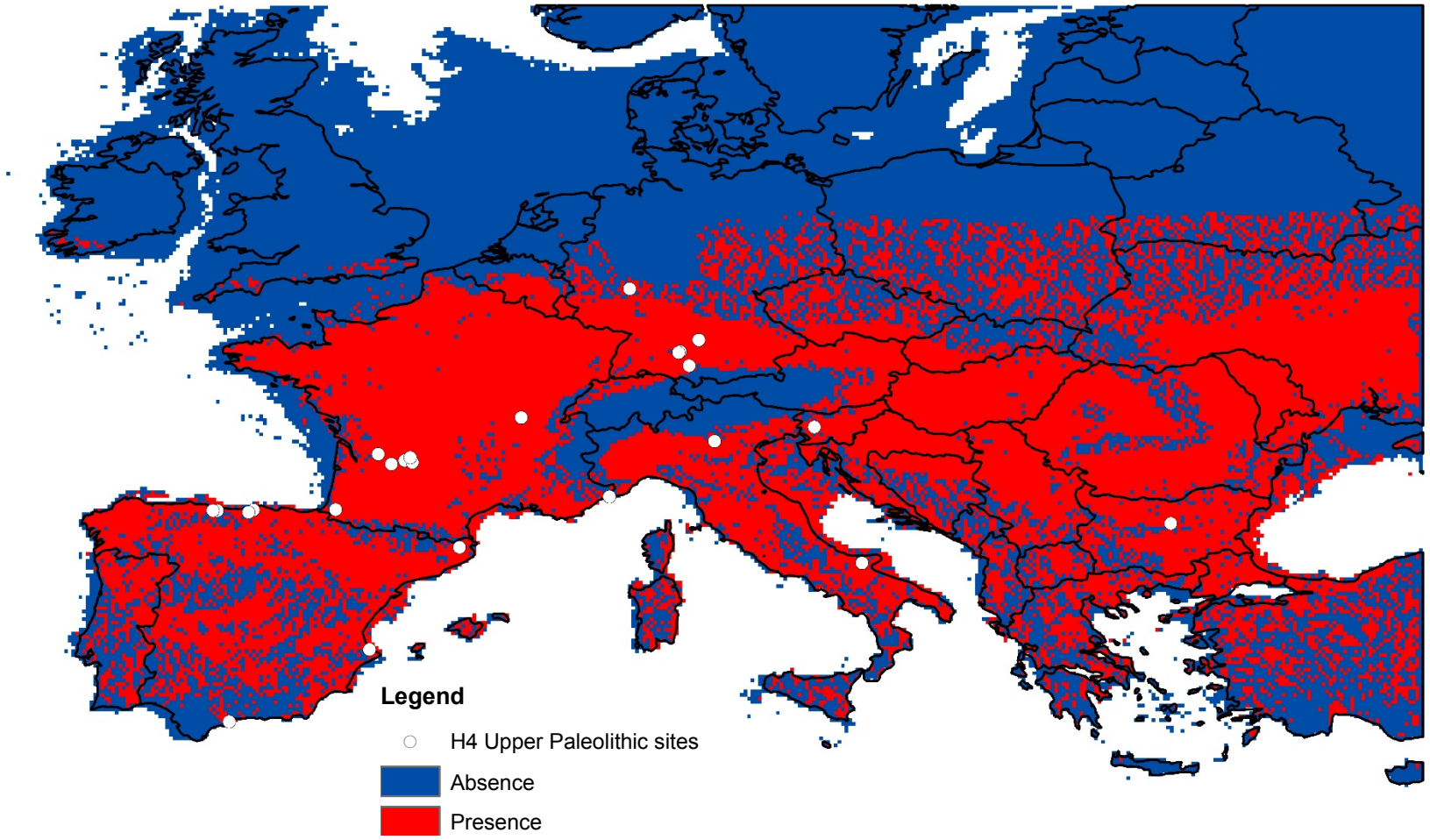

Figure 40. Maximum consensus prediction map for the H4 Upper Paleolithic exclusive model.

6.3 Post-H4 (38.6 – 36.5 ky cal BP) Predictive Models

Five sets of predictive models were generated for the Post-H4 paleoenvironmental reconstruction, dated to 38.6 – 36.5 ky cal BP (Banks et al. 2008b). These include the Middle Paleolithic exclusive, the technocomplex to fossil, the Neandertal exclusive, the Neandertal/Middle Paleolithic combined, and the Upper Paleolithic exclusive, as also seen in Sections 6.1 and 6.2 for the Pre-H4 and H4. The climate of the Post-H4, largely contemporaneous to Greenland Interstadial 8 (GI8) (Banks et al. 2008b), while still colder than present-day conditions, was not as cold as was seen during the H4 (Van Andel and Tzedakis 1996).

6.3.1 Middle Paleolithic Exclusive Consensus Prediction Model

The Middle Paleolithic archaeological sample of sites that have never produced diagnostic Neandertal remains dating to the Post-H4 consists of 10 absolutely dated sites. The *p*-value for this model, generated from Pearson's P-Value Compute (Pearson et al. 2007) equals 0.008 with a success rate of 50% (Table 38). This highly significant *p*-value indicates that the model was able to classify the known test points at a better than random rate and it is highly unlikely that the results of this model are due to random chance.

The majority prediction (Figure 41), with areas of habitat suitability classified as present if 50% or more of the *n – 1* thresholded best-subsets runs of GARP predict a pixel as present, shows a map where areas of probable presence are confined to below 47.5 degrees latitude. The area of presence is confined to the southern extremes of

Europe, mainly following the Mediterranean coastline and covering the majority of the Iberian Peninsula, the Apennine Peninsula, Greece, and the western edge of the Anatolian Peninsula. The islands of Ibiza, Menorca, Mallorca, Corsica, Sardinia, Sicily, and Crete also identify large areas of suitable habitat. The lowland areas of southern and western France are also predicted as having suitable habitat for the Middle Paleolithic exclusive sample during this paleoenvironmental reconstruction. In addition, areas following the paleo-shoreline of the Adriatic and Black Seas have large areas of suitable habitat. Seventeen percent of the study area, or 9,835 pixels, are designated present (Table 39).

The minimum prediction (Figure 42) is more geographically constricted to between 46 and 36.5 degrees latitude and only 6% of the study area predicted as showing the presence of suitable habitat (3,289 pixels) (Table 39). Even in the minimum consensus prediction map, the Ebro River Valley is well defined and large areas of the central and southeastern Iberian Peninsula are predicted present. Other areas where all replicates used to create the consensus model predict suitable habitat as present include large swaths of northern and central Iberia, southern France, Corsica, Sardinia, the Apennine Peninsula, the southern portion of the Balkan Peninsula, the western edges of the Anatolian Peninsula, and the Kocaeli and Thracian Peninsulas separating the Black Sea from the Sea of Marmara.

The maximum prediction (Figure 43) closely resembles the majority map, but has more continuous areas of where one or more of the thresholded best-subsets runs predicted the presence of suitable habitat. Twenty-two percent of the study area is

classified as such (13,013 pixels) (Table 39). This is the first model for which Middle Paleolithic presence is predicted along much of the areas presently under the sea-level. Areas classified as present on this map include the areas seen on both the preceding minimum and majority maps, as well as areas reaching into northern and central France around the western edges of the Massif Central, lowland areas running along the southern edge of the Balkan Mountains, and the southern portion of the Great Hungarian Plain.

P	0.008
Success ratio	0.5

Table 38. Pearson's *p*-value for the Post-H4 Middle Paleolithic exclusive model.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	9,835	48,416	0.17
Minimum	3,289	54,962	0.06
Maximum	13,013	45,238	0.22

Table 39. Pixel counts for majority, minimum, and maximum Post-H4 Middle Paleolithic exclusive model.

The majority, minimum, and maximum consensus prediction maps (Figure 41 – 43) for the Post-H4 Middle Paleolithic exclusive consensus model begin on the following page.

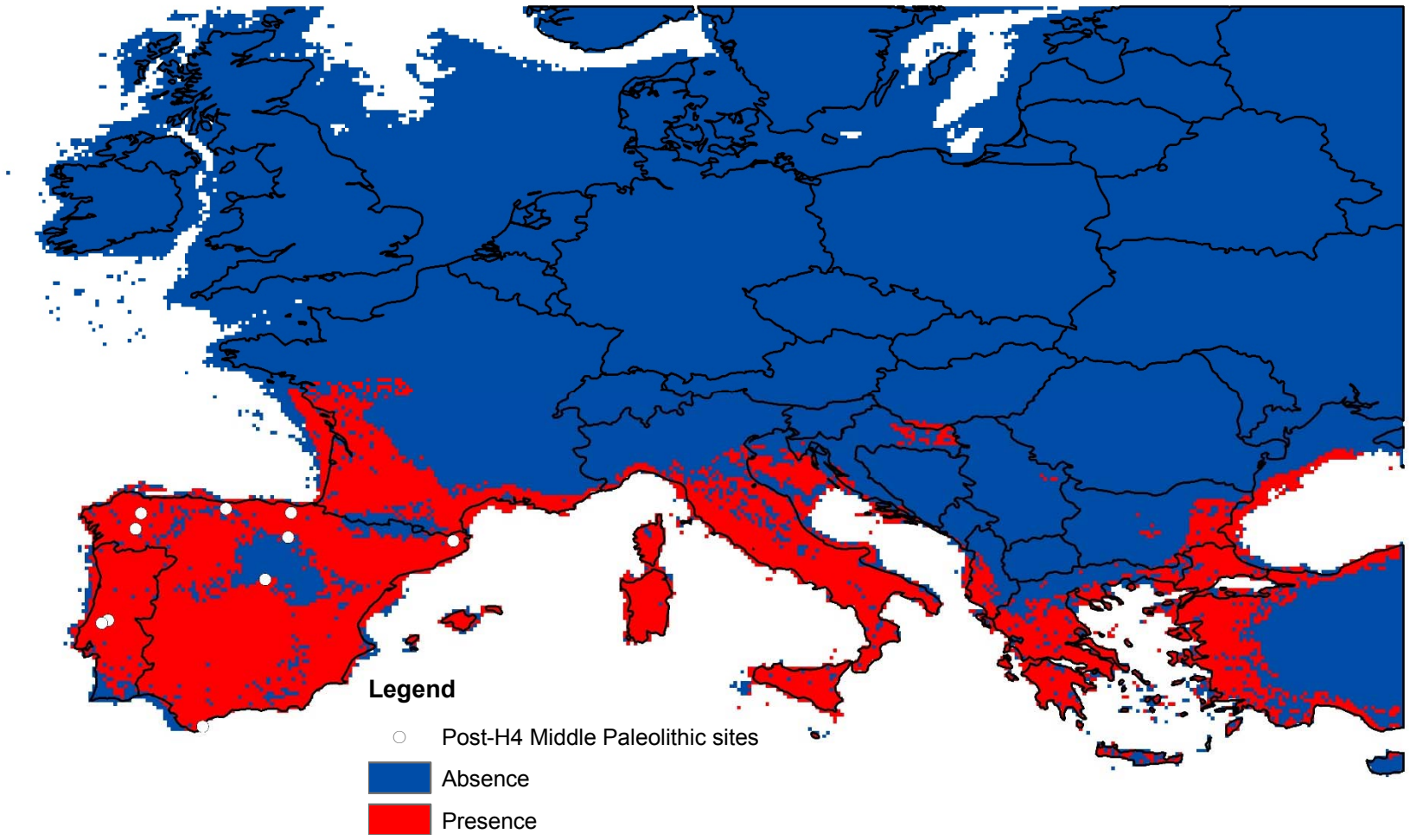

Figure 41. Majority consensus prediction map for the Post-H4 Middle Paleolithic exclusive model.

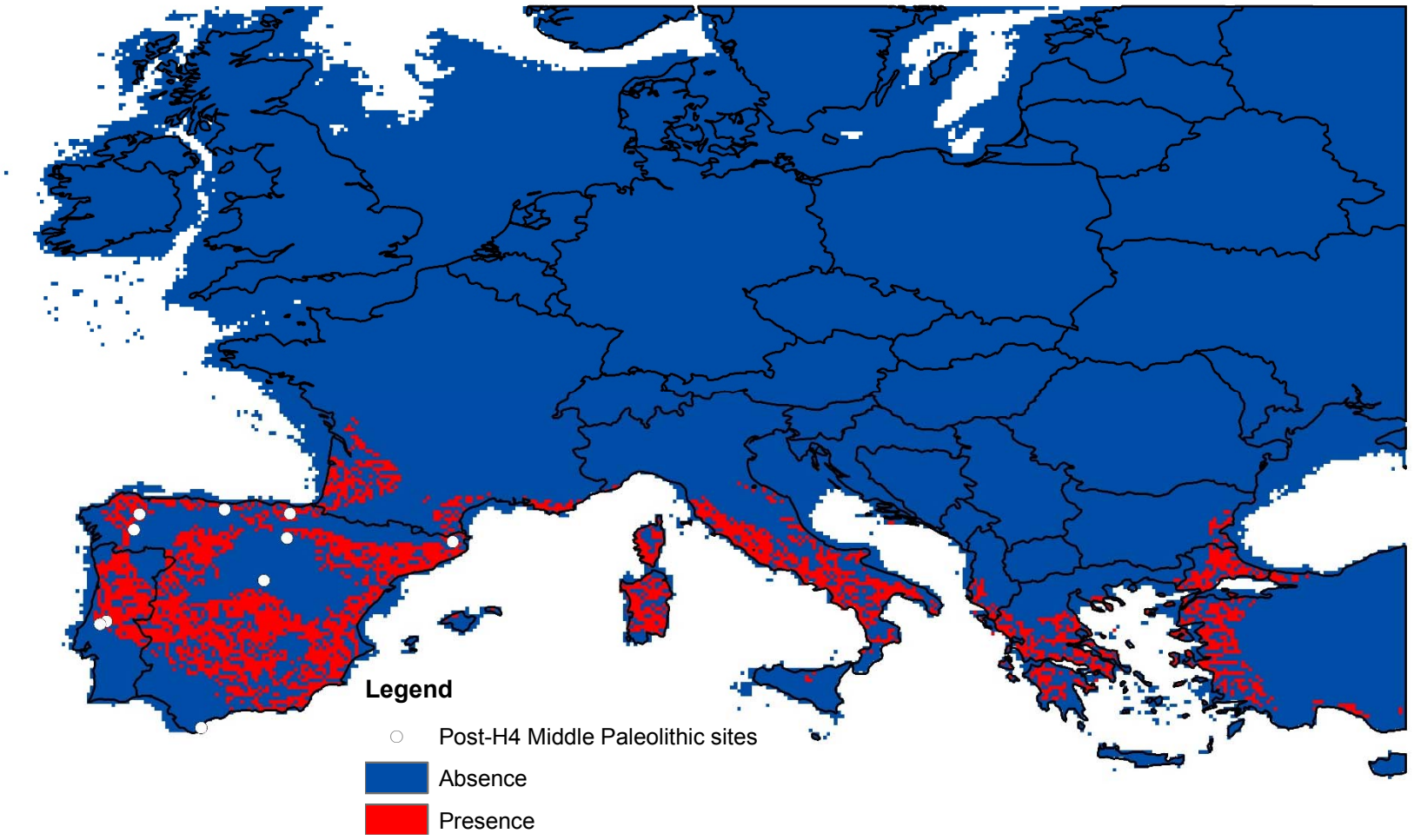

Figure 42. Minimum consensus prediction map for the Post-H4 Middle Paleolithic exclusive model.

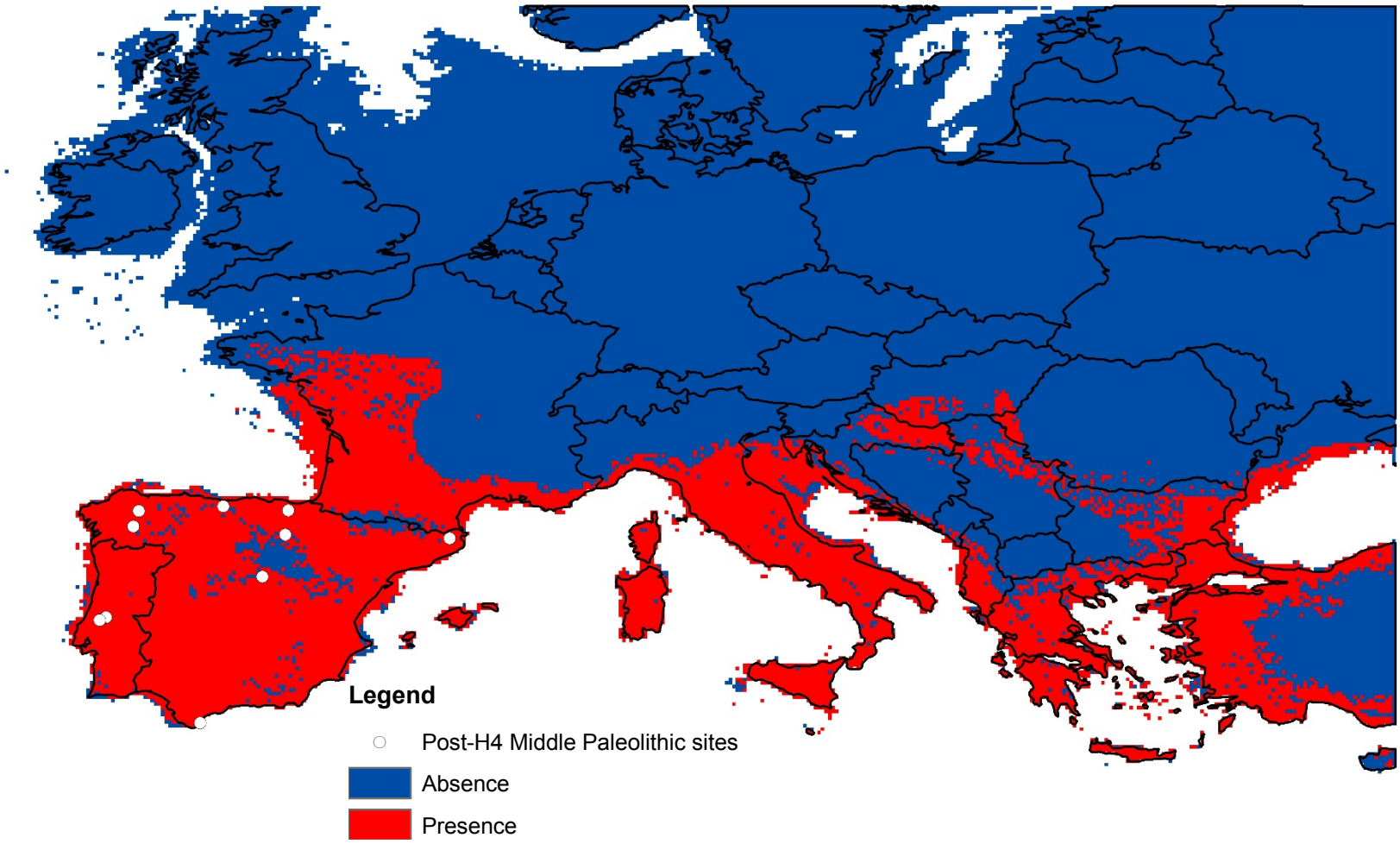

Figure 43. Maximum consensus prediction map for the Post-H4 Middle Paleolithic exclusive model.

6.3.2 Technocomplex to Fossil Consensus Prediction Model

For the Post-H4 reconstruction, the following model was calibrated with Middle Paleolithic sites dating to the Post-H4 (n = 10), but asked to correctly classify known locations of contemporaneous Neandertal remains (n = 5). After thresholding, the model had a success rate of 80%, where 4 out of 5 test points were correctly classified as present. The test point that was not correctly identified by the model was the Gibraltar site complex. A standard cumulative binomial probability was used to generate the consensus p-value for the thresholded model, here p = 0.0001 (Table 40). This value indicates that the model created with Post-H4 Middle Paleolithic sites was able to predict known locations with Neandertal remains at a better than random rate and the null hypothesis that these results happened at random is rejected. The only site the model was not able to correctly classify as present was the site of Vindija Cave, located in modern northern Croatia. Twelve percent of the study area was identified where there was suitable habitat, or 7,213 pixels.

The map of the thresholded results for this model (Figure 44) is extremely similar to the majority consensus prediction map seen for the Middle Paleolithic exclusive sample during the same period. The presence of suitable habitat is predicted across most of the Iberian Peninsula, southernmost France, the Mediterranean coastline, the Apennine Peninsula, the southern reaches of the Balkan Peninsula, the western and southern portions of the Anatolian Peninsula, the paleo-shoreline of the Black Sea, the majority of the Adriatic Shelf, and the major islands in the Mediterranean (including Crete).

The Partial-ROC scores were calculated for the unthresholded prediction (Table 41). The probability (*P*) that the mean is ≤ 1.0 is exceedingly small and is significantly elevated above random expectations. The map of the unthresholded results of this model illustrates the full range of geographic areas predicted as having suitable habitat by one or more of the 10 individual models gathered by the best-subsets run. Many models are also in agreement that there is suitable habitat through central France, excepting the Massif Central. The un-thresholded prediction map (Figure 45) shows the majority of the best subsets models used to create the consensus maps are predicting probable presence of suitable habitat in the southernmost portions of Europe. High concentrations of model agreement appear in the Iberian Peninsula, southern France, the Apennine Peninsula, the southern Balkan Peninsula, and the westernmost edges of the Anatolian Peninsula.

P	0.0001
Critical Binomial Value	2
Test points correctly classified as present	4
Success ratio	0.8

Table 40. Validation for Post-H4 technocomplex to fossil model.

Minimum	1.64
Maximum	1.88
Mean	1.78
SD	0.10
Replicates ≤ 1	0
Z-statistic	234.60
P	5.92×10^{-14}

Table 41. Partial-ROC results for the Post-H4 technocomplex to fossil model.

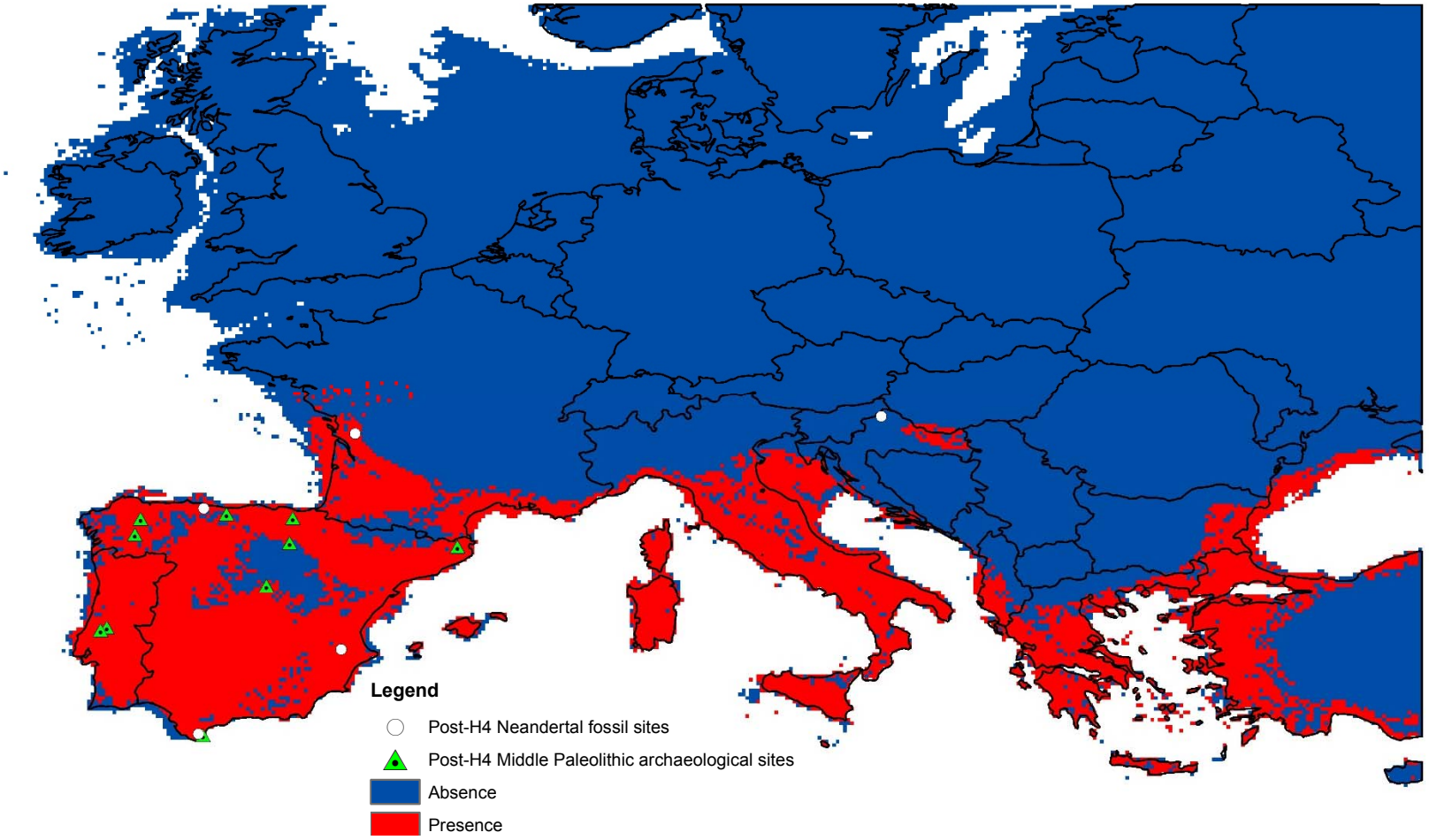

Figure 44. Thresholded consensus prediction map for the technocomplex to fossil model, generated with Middle Paleolithic archaeological sites (*n* = 10) and validated Neandertal fossil locations (*n* = 5) for the Post-H4.

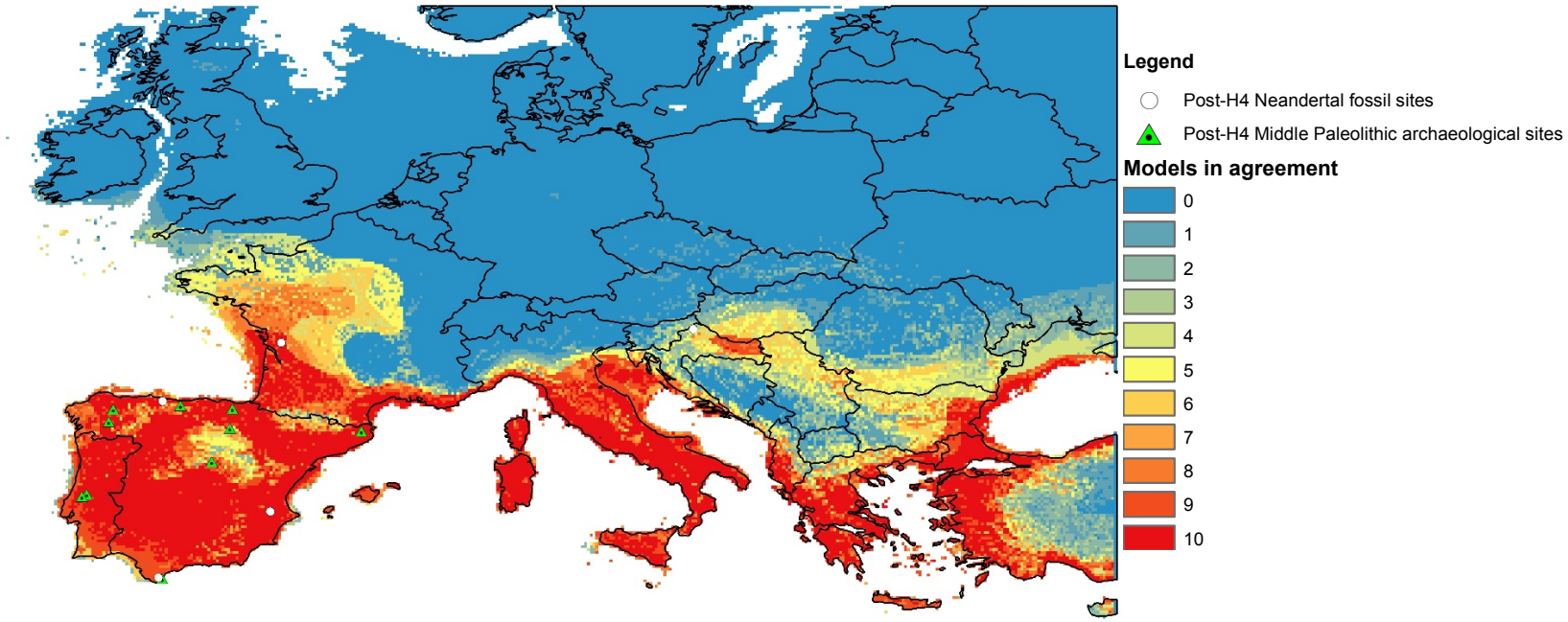

Figure 45. Unthresholded consensus prediction map for the technocomplex to fossil model, generated with Middle Paleolithic archaeological sites (*n* = 10) and validated Neandertal fossil locations (*n* = 5) for the Post-H4.

6.3.3 Neandertal Exclusive Consensus Prediction Model

Neandertal remains absolutely dated to the Post-H4 (n = 5) make up the smallest sample in this project. As with the previous H4 Neandertal sample, even though this sample size is smaller than is typically used in ecological research, this project sought to determine if a statistically accurate model could be generated from the available data. A standard $n - 1$ procedure was used, which resulted in 5 total $n - 1$ replicates run through GARP and 50 best subsets models (10 per replicate) for processing. Pearson's P-value Compute (Pearson et al. 2007) generated the consensus p-value of 0.35 and success rate of 20% (1 out of 5 test points correctly classified) (Table 42). The only site the model was able to correctly predict was El Sidrón. The other four sites in the sample were incorrectly classified as absent (Devil's Tower, Cova Forradá, St. Cesaire, and Vindija).

Since GARP is an iterative process, meaning each time the algorithm is run a different answer can potentially be reached, the experiment was run a second time to examine if a model that could predict known test points at a better than random rate could be achieved with this data. The second run resulted in a model that produced a Pearson's p-value score of 0.06 and a success rate of 0.4, or correctly classifying 2 out of 5 test points (Table 44). Despite doubling the success rate, the second consensus model cannot be shown to predict known test points at a better than random rate and so the null hypothesis could not be rejected. Therefore, the conclusion must be drawn that this model's predictions may be due to random chance. Despite the failed experiment, the result were included in this dissertation. The failed results are likely largely due to the extremely small size of this sample. While GARP has been demonstrated to reach 90%

of its power at 9 presence points (Stockwell and Peterson 2002b), samples that fall below that point may not be large enough to create truly rigorous models (Pearson et al. 2007). Pixel counts for the majority, minimum, and maximum consensus prediction maps of the first failed run (Figures 46 – 48) are included in Table 43 and for the second failed run (Figures 49 – 51) in Table 45.

P	0.346626
Success ratio	0.2

Table 42. Validation for the Post-H4 Neandertal exclusive model, run 1, showing non-significant results.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	5,977	52,274	0.10
Minimum	647	57,604	0.01
Maximum	13,538	44,713	0.23

Table 43. Pixel counts and ratios for the majority, minimum, and maximum predictions of the Post-H4 Neandertal exclusive model, non-significant run 1.

P	0.06
Success ratio	0.4

Table 44. Statistical validation for 2nd non-significant run of the Post-H4 Neandertal exclusive model.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	4,237	54,014	0.07
Minimum	458	57,793	0.008
Maximum	10,302	47,949	0.18

Table 45. Pixel counts for the 2nd non-significant run of the Post-H4 Neandertal exclusive model.

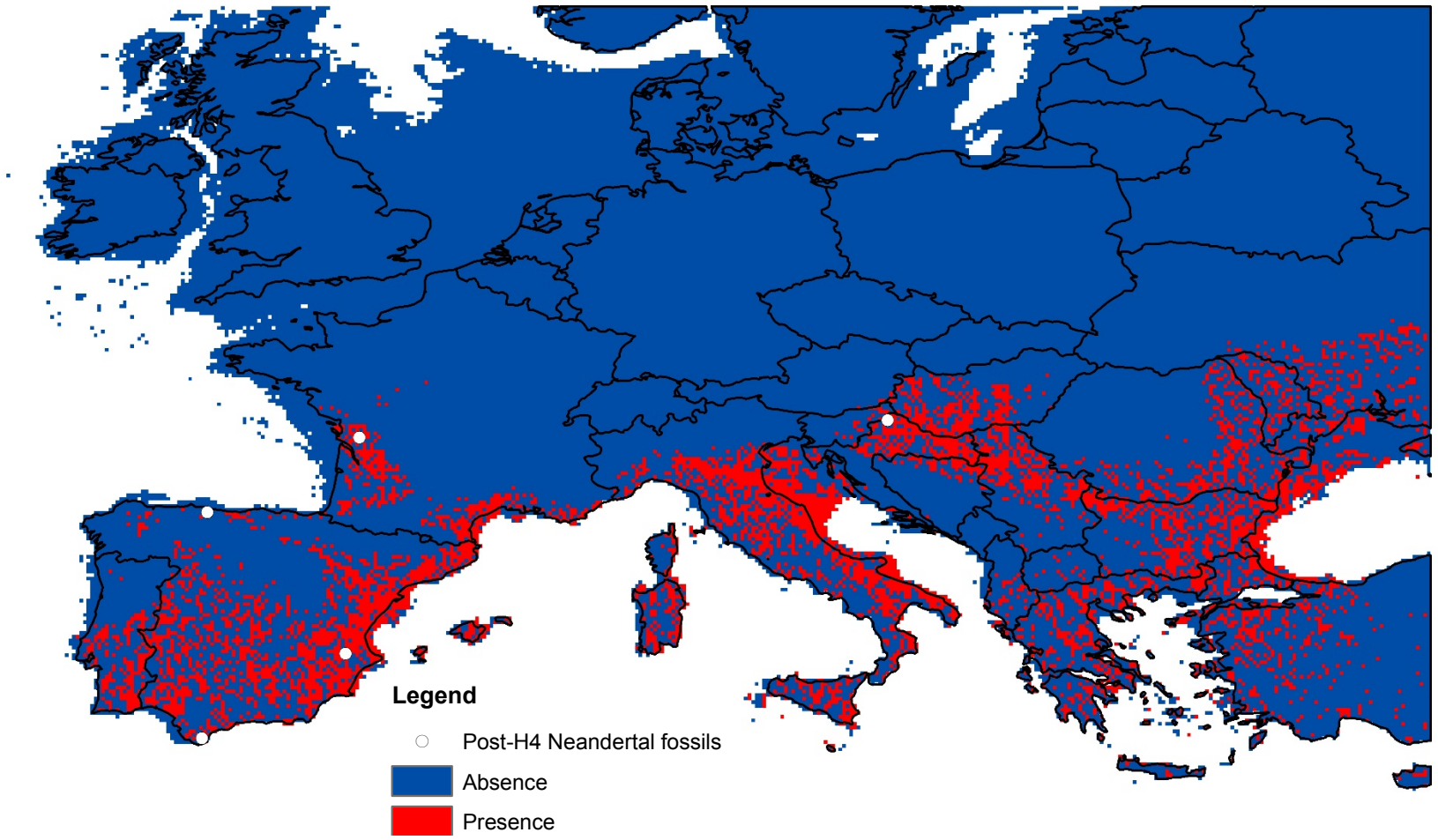

Figure 46. Majority consensus prediction map for the Post-H4 Neandertal exclusive model, run 1 (non-significant).

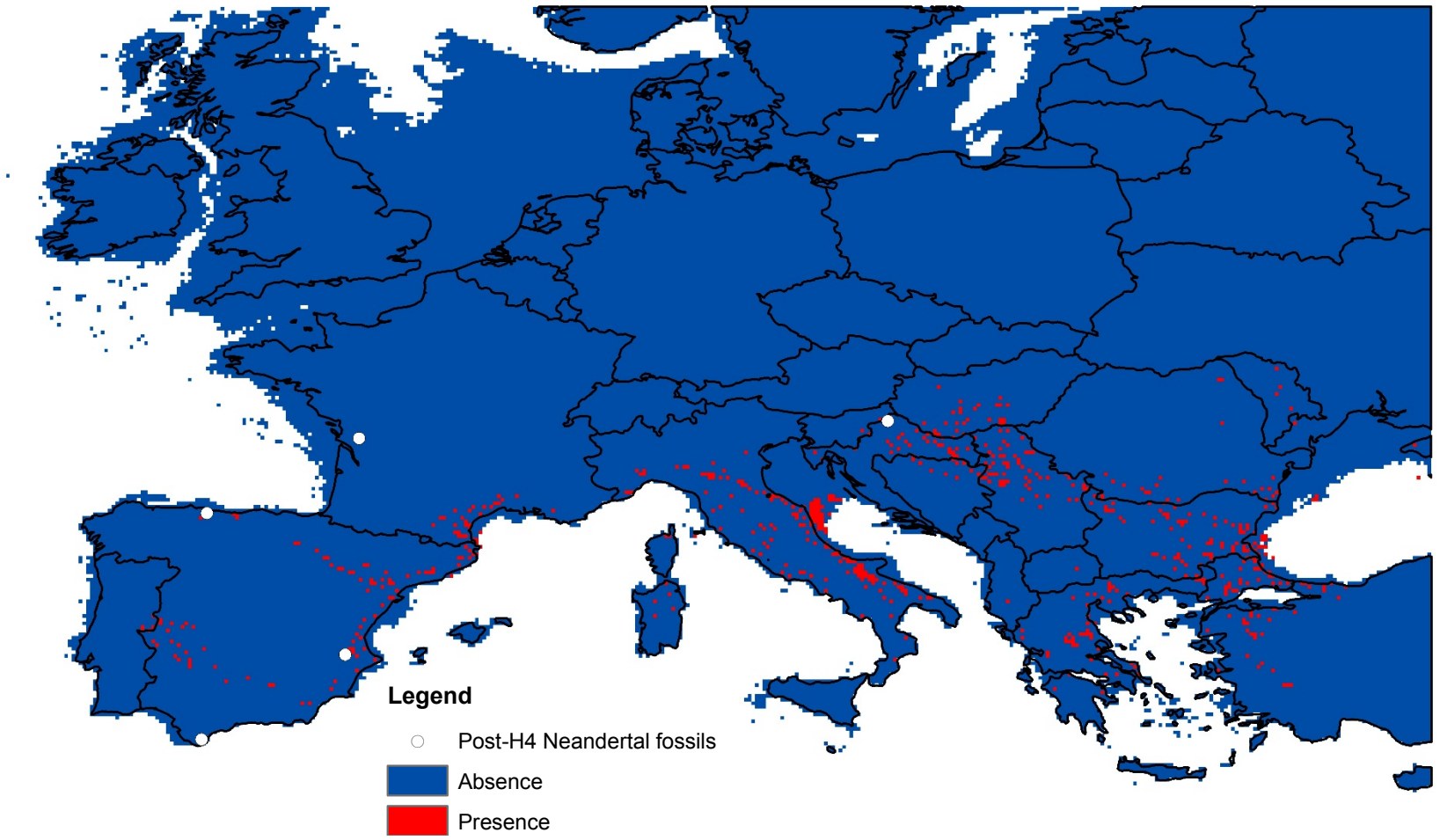

Figure 47. Minimum consensus prediction map for the Post-H4 Neandertal exclusive model, run 1 (non-significant).

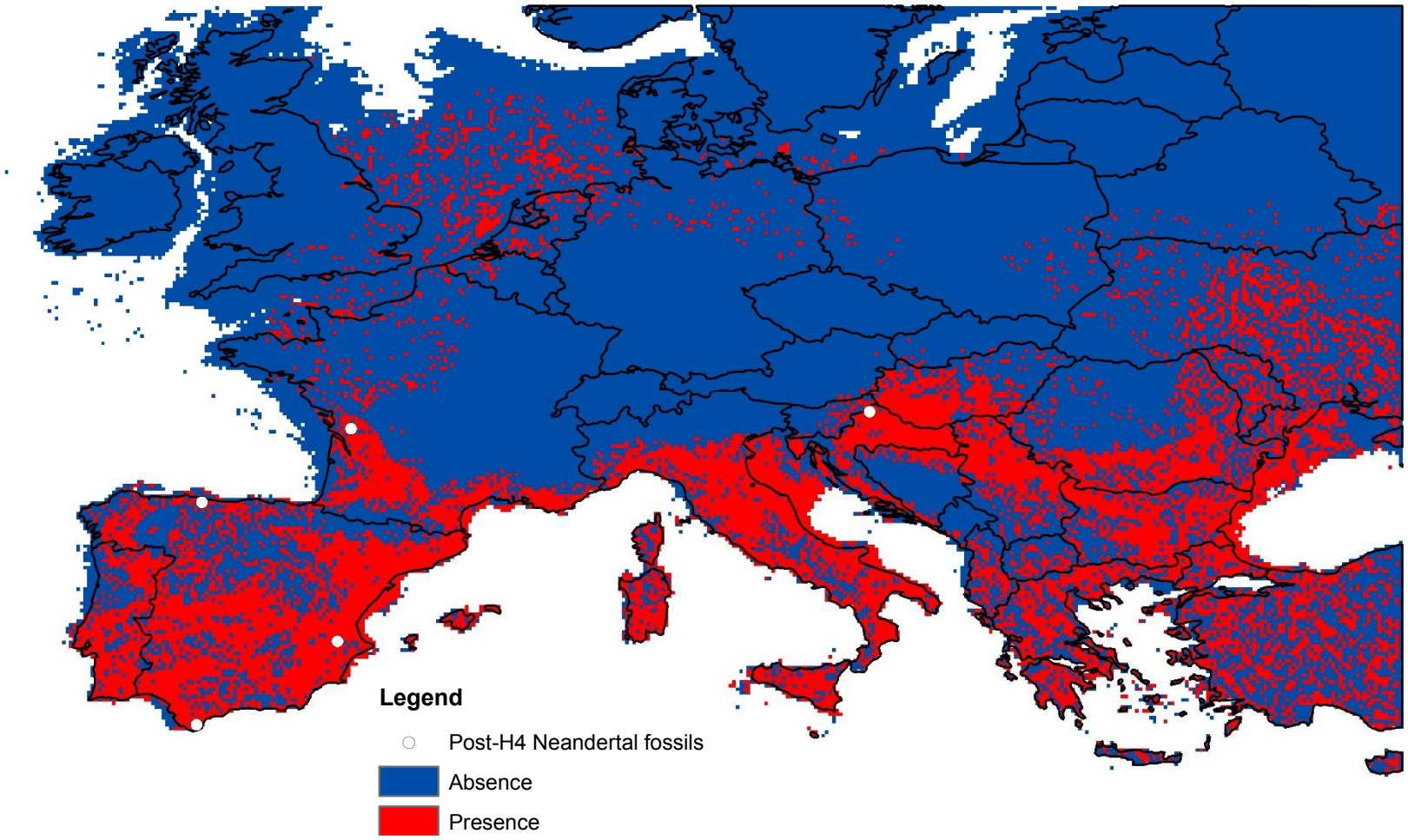

Figure 48. Maximum consensus prediction map for the Post-H4 Neandertal exclusive model, run 1 (non-significant).

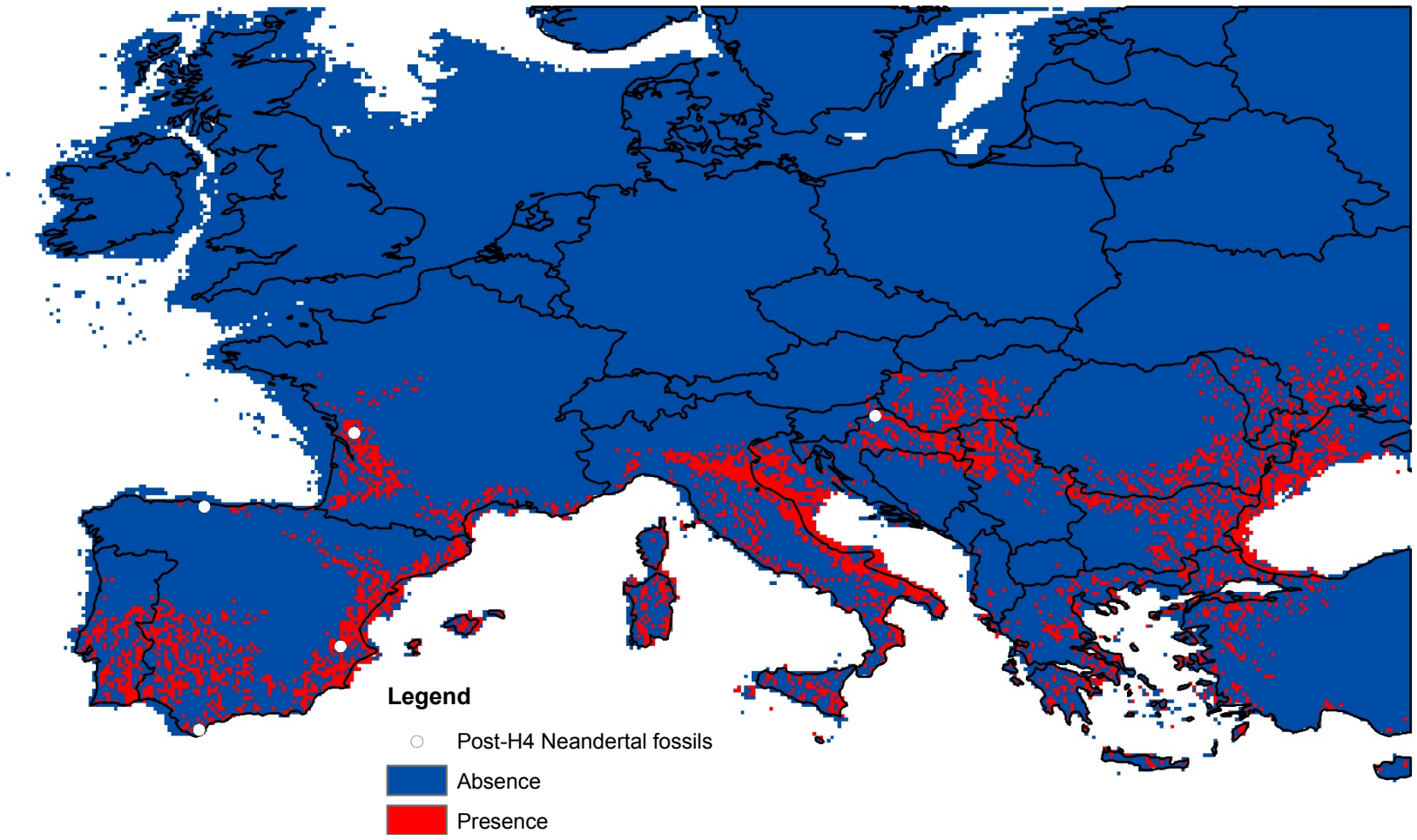

Figure 49. Majority consensus prediction map for Post-H4 Neandertal exclusive model, run 2 (non-significant).

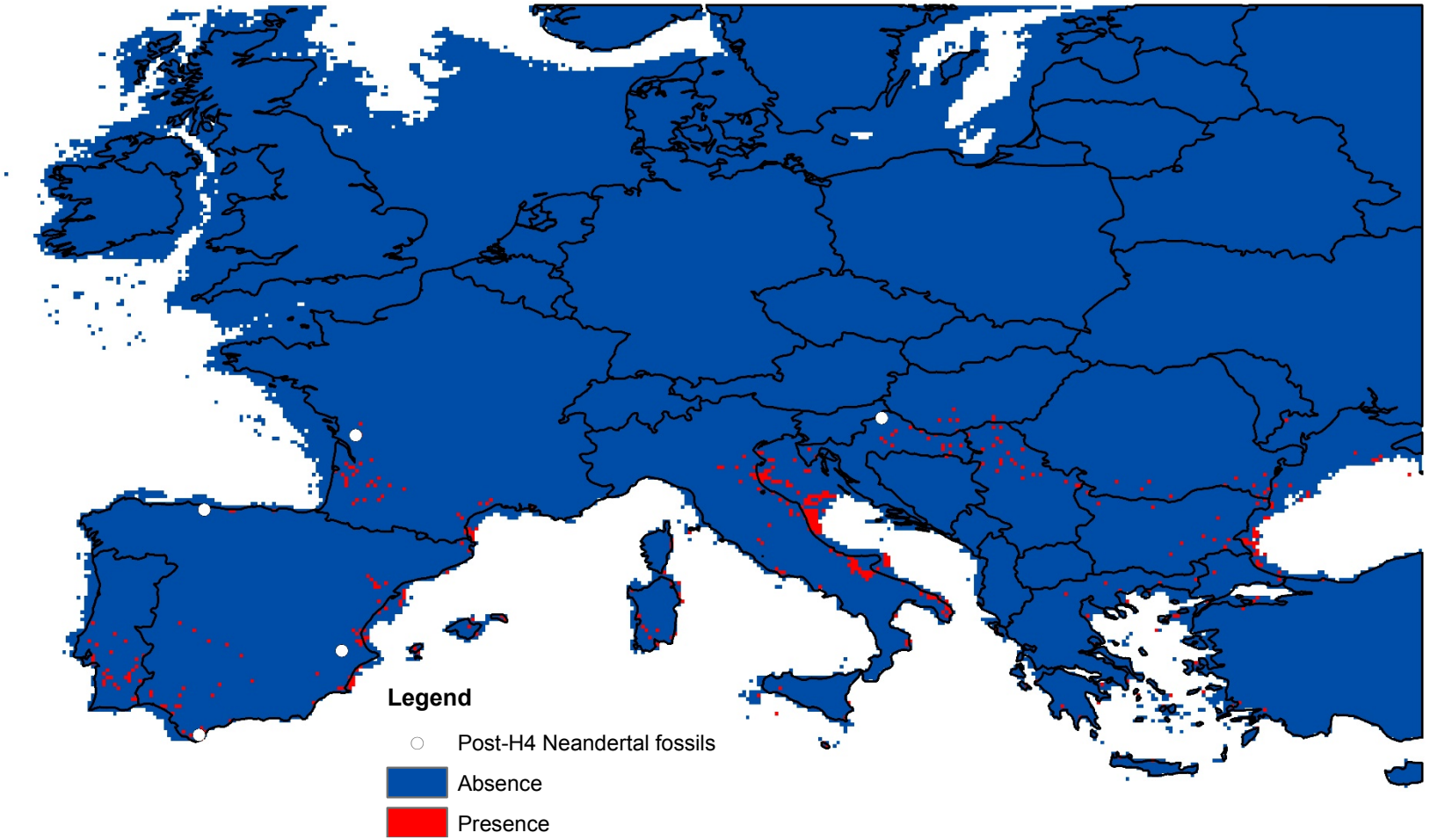

Figure 50. Minimum consensus prediction map for the Post-H4 Neandertal exclusive model, run 2 (non-significant).

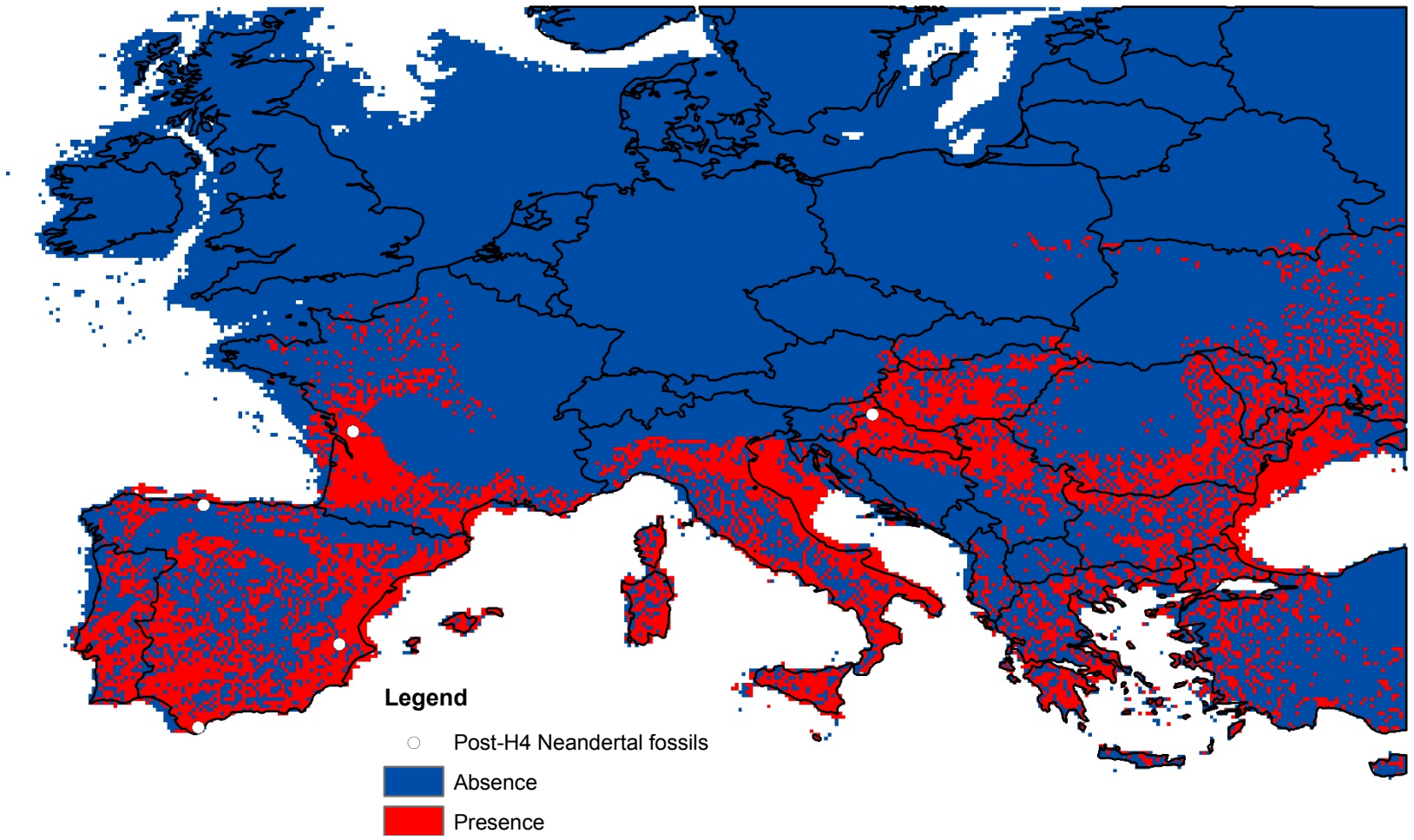

Figure 51. Maximum consensus prediction map for the Post-H4 Neandertal exclusive model, run 2 (non-significant).

6.3.4 Neandertal Fossil and Middle Paleolithic Archaeological Combined Sample

Since the Neandertal exclusive sample failed to yield statistically significant models that could correctly classify known test points better than random chance would allow, the results of the consensus prediction model for the Neandertal/Middle Paleolithic combined sample (n = 15) were considered especially important by this study. The sample size tripled when compared to the Neandertal exclusive sample for the same time period, covered in the previous section (6.3.3). The p-value for this model (via Pearson's p-value) equaled 0.0002 with a success rate of 66%, or 10 of 15 test points correctly classified as present (Table 46). These values indicate that this model predicted known test points at a better than random rate and the null hypothesis that these results occurred due to random chance can be rejected.

The majority consensus prediction map (Figure 52) shows areas of habitat suitability that are similar to the results of the Neandertal/Middle Paleolithic combined experiment of the preceding H4, despite the warmer climate of the Post-H4. Largely continuous areas throughout southern Europe are predicted present, but all areas north of the Alps lack suitable habitat. The lowlands of western and southern France, north of the Pyrenees and the Ebro River Valley are predicted as present. Other significant areas where suitable habitat is indicated to be present by 50% or more of the thresholded best-subsets runs include the entire Apennine Peninsula south of the Alps, nearly the entirety of the Adriatic Shelf, the southernmost portion of the Balkan Peninsula (including mainland Greece and the Peloponnese), portions of the Great Hungarian Plain, the exterior of the Anatolian Peninsula, areas of the Black Sea shelf, the eastern portions of

the Danube River Valley, and the major islands of the Mediterranean. The area predicted present covers 23% of the total study area (13,584 pixels) (Table 47).

The minimum consensus prediction map (Figure 53), again the most conservative view of this model, is confined to the southern extremes of Iberia, the Ebro River Valley, portions of southern France, the Mediterranean coastline of France and Italy, the central Apennine Peninsula, Ibiza, Mallorca, Menorca, Sardinia, Sicily, and a few isolated spots in the southern Great Hungarian Plain, the Balkan Peninsula, the Grecian Peloponnese, Bulgaria, and northern Turkey along the shoreline of the Black Sea. Only 6% of the total study area shows the presence of suitable habitat (3,554 pixels) (Table 47). The maximum prediction map (Figure 54) classifies 30% of the study area as present (17,374 pixels) (Table 47) and greatly resembles the majority map, with more contiguous areas predicted present.

P	0.0002
Success ratio	0.66

Table 46. The results of Pearson's *p*-value for the Neandertal/Middle Paleolithic combined consensus prediction model during the Post-H4.

	Pixels predicted present	**Pixels predicted absent**	**Ratio of present/total**
Majority	13,584	44,667	0.23
Minimum	3,554	54,697	0.06
Maximum	17,374	40,877	0.30

Table 47. Pixel ratios for the majority, minimum, and maximum prediction maps for the Neandertal/Middle Paleolithic combined consensus prediction model during the Post-H4.

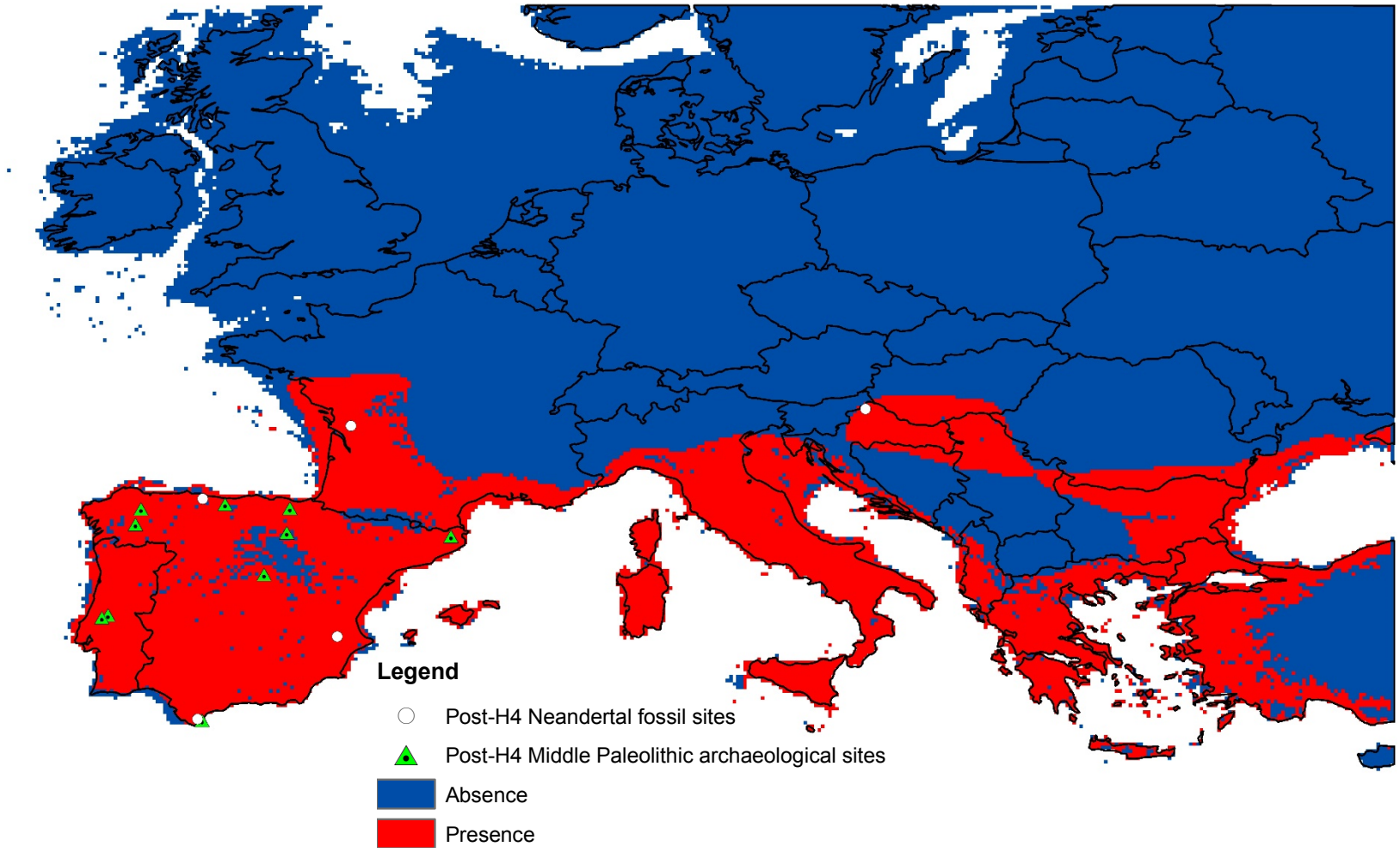

Figure 52. Majority consensus prediction map for the model generated with the combined sample of Neandertal fossil locations (*n* = 5) and Middle Paleolithic archaeological sites (*n* = 10) during the Post-H4.

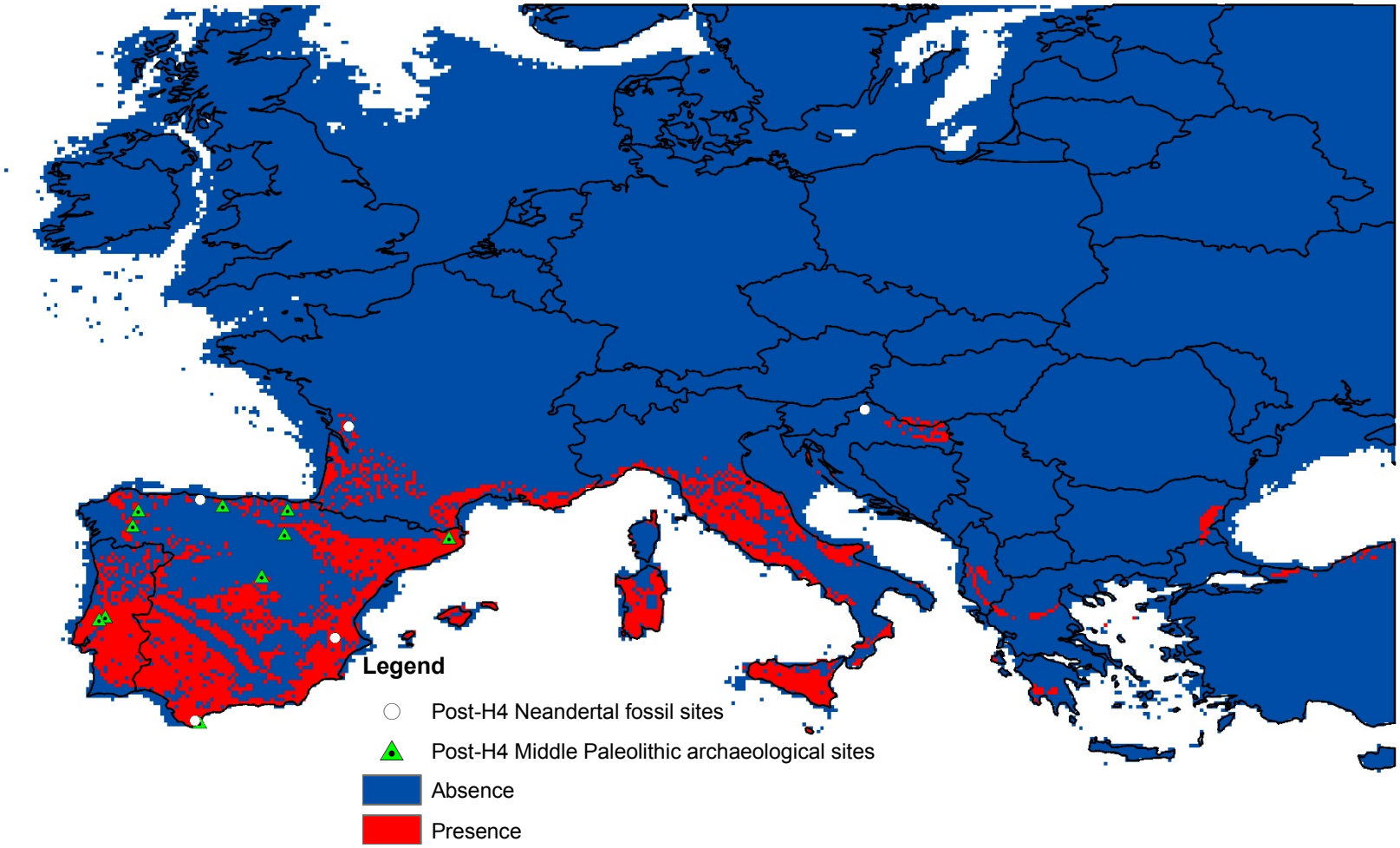

Figure 53. Minimum consensus prediction map for the model generated with the combined sample of Neandertal fossil locations (*n* = 5) and Middle Paleolithic archaeological sites (*n* = 10) during the Post-H4.

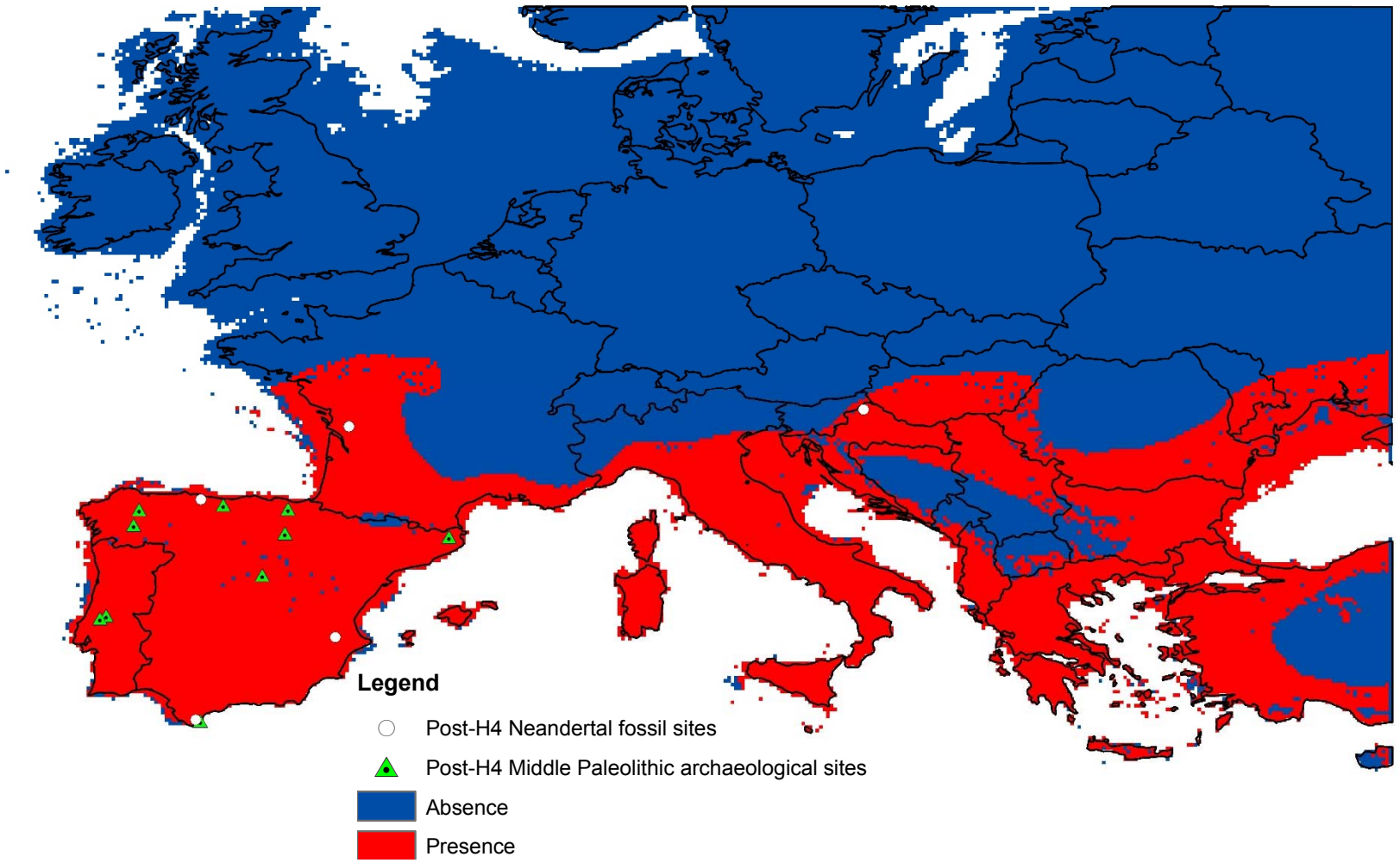

Figure 54. Maximum consensus prediction map for the model generated with the combined sample of Neandertal fossil locations (*n* = 5) and Middle Paleolithic archaeological sites (*n* = 10) during the Post-H4.

6.3.5 Upper Paleolithic Exclusive Consensus Prediction Model

The predictive model created for the Post-H4 paleoenvironmental reconstruction with a UP exclusive sample of locations (n = 31) was the largest of the Upper Paleolithic samples included in this dissertation. All p-values derived from cumulative binomials were ≤ 0.0001 (Table 48). All Partial-ROC probability scores were significantly elevated above random expectations, less than or equal to 0.03 (Table 49). The null hypothesis of reaching these results via random chance is therefore rejected.

The majority map (Figure 55) predicts presence between 53.5 and 37 degrees latitude and excludes the southwestern corner of the Iberian Peninsula and the Alps. However, the Ebro River Valley shows a complimentary environment to what is found at contemporaneous archaeological sites dated to the Post-H4. The majority of modern France, central Germany, the Great Hungarian Plain, and the lowland areas surrounding the Carpathians are also predicted present. Other significant areas where 50% or more of the thresholded best-subsets runs indicate the presence of suitable habitat for early modern humans (EMHs) during the Post-H4 include: areas on the Iberian Peninsula south of the Ebro River Valley, the Po River Valley, the Balkan Peninsula, southern England, and the Anatolian Peninsula. The outline of the Alps, the Pyrenees, and Carpathian Mountains are visible with few inclusions of suitable habitat within their borders. Twenty-eight percent of the total study area is predicted as present (16,108 pixels) (Table 50).

The minimum map (Figure 56) predicts presence between a more restricted 51.8 and 37.9 degrees latitude in comparison to the majority and maximum prediction maps.

Only 10% of the total study area is predicted present (5,799 pixels) (Table 50). The majority of the suitable habitat on the minimum map is found in France, following the western and northern extent of the Alps into southern Germany. Other areas of suitable habitat include: the Ebro River Valley, scattered pixels south of that point, southern England, the western and northern edges of the Great Hungarian Plain, and other small areas on the Apennine and Balkan Peninsulas.

In contrast, the maximum prediction map (Figure 57) presence is bounded by 55 and 36.5 degrees latitude and 49% of the total study area is predicted present (29,261 pixels) (Table 50). The maximum prediction, the least conservative analysis, only excludes the Alps, the Pyrenees, the southwestern coast of Iberia, the Apennine Valley, and the paleo-coastline north of the Black Sea from the areas predicted as present. Additional areas predicted as present on the maximum map that were not seen on the majority and minimum maps include: central and southern England, Wales, the Republic of Ireland, large portions of the English Channel, Sicily, increased areas of Corsica and Sardinia, and a much larger area covering the Iberian Peninsula except for the coastal areas from Lisbon to Gibraltar.

Evaluation replicates	**P-value**	**Critical Binomial Value**	**Success ratios**
Evaluation set 1	2.22×10^{-5}	6	0.625
Evaluation set 2	9.00×10^{-5}	7	0.6875
Evaluation set 3	4.328×10^{-5}	9	0.8125
Evaluation set 4	0.0001	6	0.625
Evaluation set 5	3.98×10^{-6}	9	0.875

Table 48. Cumulative binomial probabilities for thresholded predictions, Post-H4 Upper Paleolithic exclusive model.

	1	2	3	4	5
Minimum	1.16	0.90	1.01	0.63	1.23
Maximum	1.81	1.73	1.69	1.77	1.72
Mean	1.56	1.46	1.48	1.36	1.60
SD	0.13	0.15	0.15	0.20	0.09
Replicates ≤ 1	0	4	0	37	0
Z-statistic	141.45	98.056	99.42	58.39	215.61
P	3.86×10^{-6}	0.001	0.0008	0.03	4.61×10^{-12}

Table 49. Partial-ROC scores for the Post-H4 Upper Paleolithic exclusive model.

	Pixels predicted present	Pixels predicted absent	Ratio of present/total
Majority	16,108	42,143	0.28
Minimum	5,799	52,452	0.10
Maximum	28,630	29,261	0.49

Table 50. Pixel ratios for the Post-H4 Upper Paleolithic exclusive model.

The majority, minimum, and maximum consensus prediction maps for the Post-H4 Upper Paleolithic exclusive model begin on the following page.

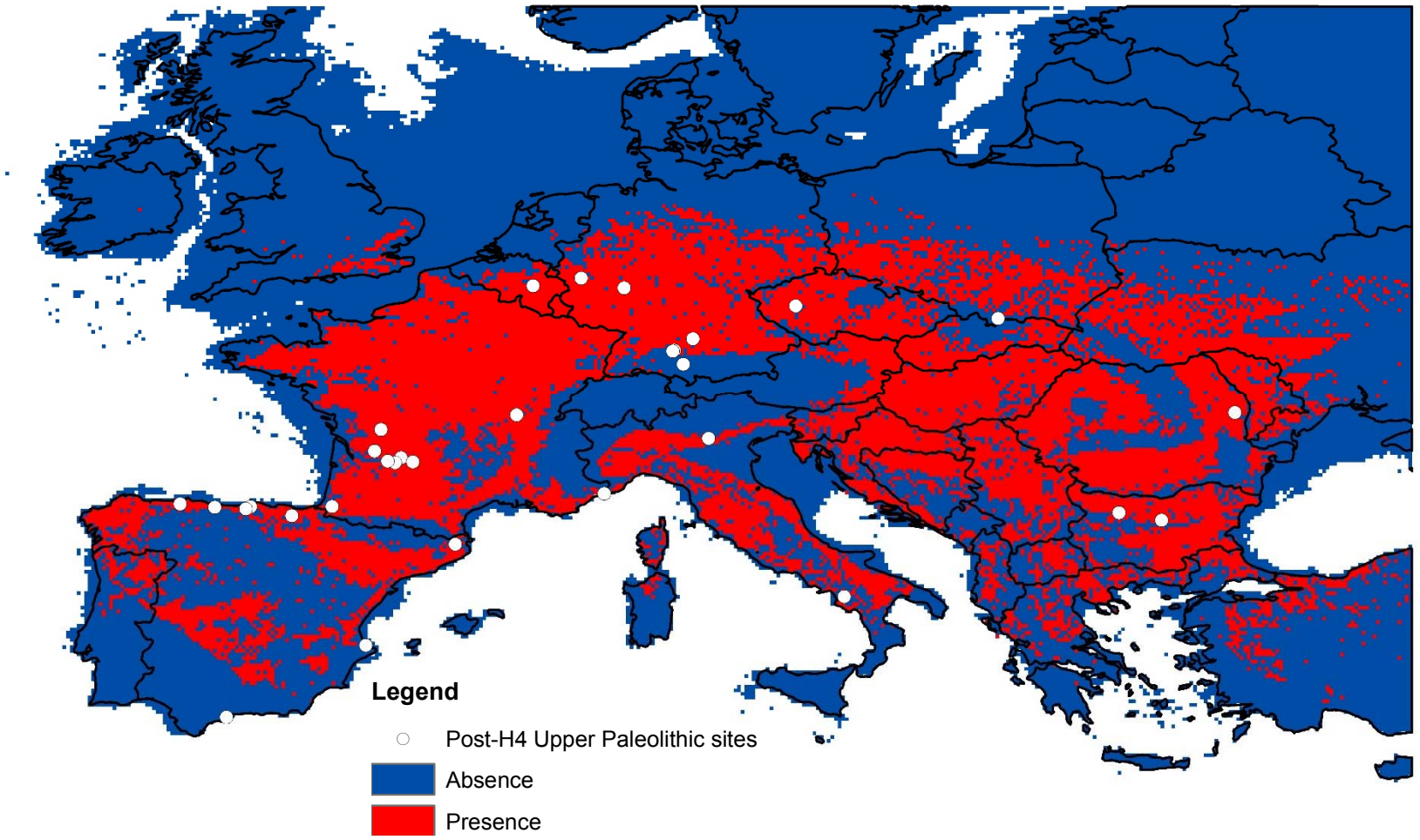

Figure 55. Majority consensus prediction map for the Post-H4 Upper Paleolithic exclusive model.

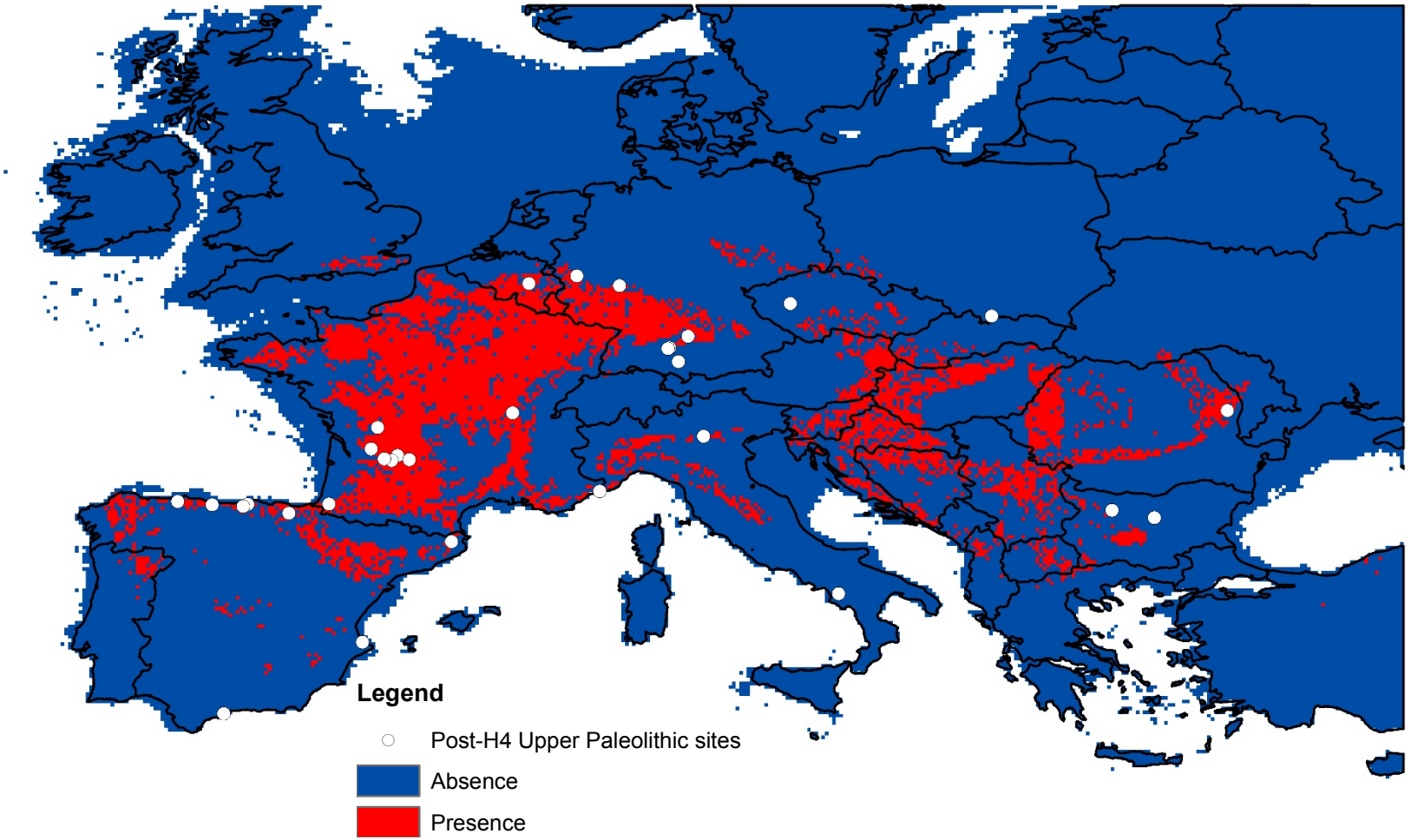

Figure 56. Minimum consensus prediction map for the Post-H4 Upper Paleolithic exclusive model.

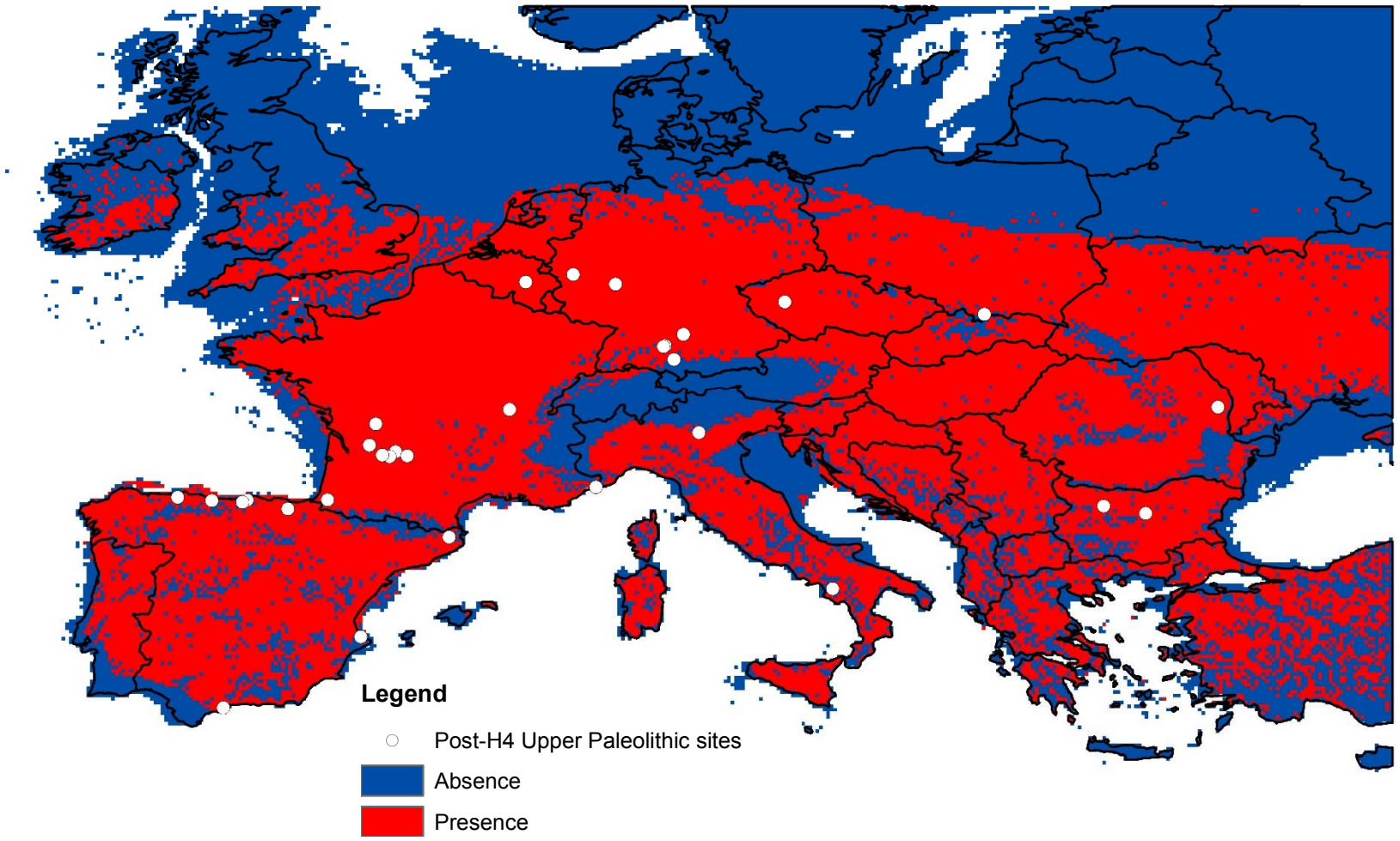

Figure 57. Maximum consensus prediction map for the Post-H4 Upper Paleolithic exclusive model.

6.4 Overlap Analysis

The following section consists of the results of a spatial geographic overlap analysis. The analysis was confined to predictions from the same environmental reconstruction. Pixels displayed in red on the following maps illustrate the exact geographic extent of the overlap between majority prediction maps. In other words, pixels classified as red were predicted as present by both models undergoing comparison. This method allows for a direct way to examine the geographic extent of the suitable habitat between two disparate samples and offers insight into the areas where different populations could have come into contact with one another.

The results for the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive for the Pre-H4, H4, and Post-H4 were compared. Only the majority prediction maps were used in this analysis, instead of the maximum and minimum, as they offer a compromise between the most and least conservative predictions generated by the previous experiments and give a good view of the extent of overlapping suitable habitat for Late Neandertals and early modern humans (EMHs). This analysis offers great insight into addressing the questions this dissertation has on the extent and fluctuation of that area through time.

6.4.1 Pre-H4 Overlap

The geographic area predicted present for suitable habitat in both models, of the exact extent of the geographic overlap for the majority maps for the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive consensus Pre-H4 models,

consists of 12,011 pixels, or 21% percent of the total study area. The largest and most continuous cluster of overlap in suitable habitat predictions is again found in the western and central areas of modern France, the Ebro River Valley, large areas of northwestern and central Iberia, the Apennine Peninsula, the Po River Valley, Sardinia, the Great Hungarian Plain, the Transylvanian region of Romania, the Moldova, and the Dnieper Uplands. The extent of this overlap reaches far south on the Iberian Peninsula, contrary to the hypotheses put forth by the Ebro Frontier Model. These models attempting to reconstruct Neandertal and EMH presence show the largest amount of overlap during the Pre-H4. This overlap covers 83% of the EMH majority consensus prediction and only 58% of the Neandertal/Middle Paleolithic combined majority consensus prediction. This result indicates that it is ***highly likely*** EMHs encountered Late Neandertals during the Pre-H4 for the majority of their distribution. The overlap between the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive consensus prediction models during the Pre-H4 is illustrated in Figure 58.

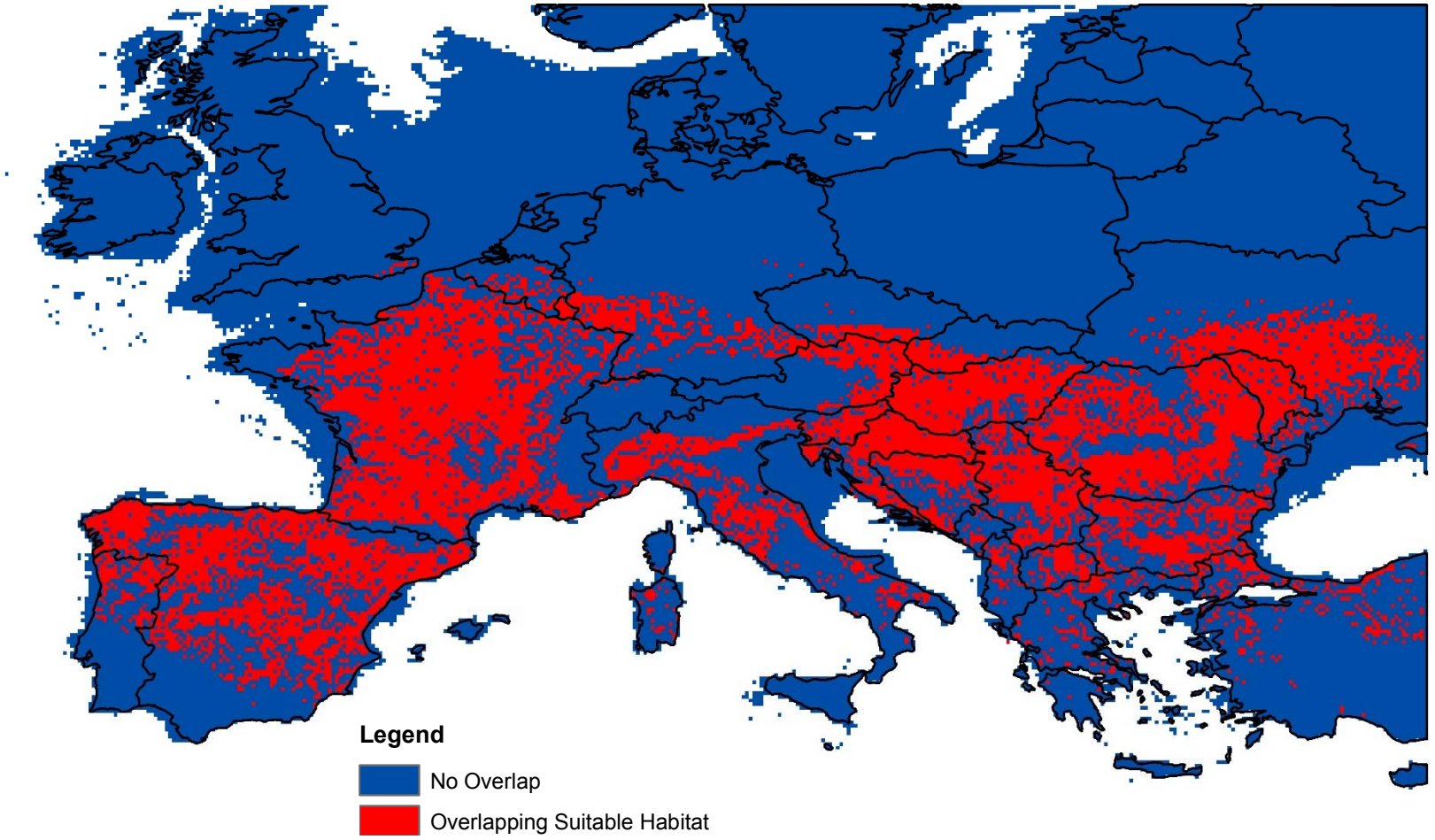

Figure 58. Geographic overlap of pixels predicted present by the majority consensus prediction maps for both the combined Neandertal fossil/Middle Paleolithic archaeological and the Upper Paleolithic during the Pre-H4.

6.4.2 H4 Overlap

The overlap between the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive consensus prediction models during the H4 is illustrated in Figure 59. The geographic area predicted present for suitable habitat in both models consists of 11% percent of the total study area or 6,279 pixels. This area covers 54% of the Neandertal/Middle Paleolithic combined majority consensus prediction and only 44% of the Upper Paleolithic exclusive. This is in contrast to the overlap analysis for the Pre-H4 where the overlap in suitable habitat generated by the majority maps made up a larger part of the Upper Paleolithic range than the Neandertal/Middle Paleolithic. The overall extent of the overlap also drops by 10% during the H4 from the previous time period.

The northern and southern latitudinal bounds of the overlap match that of the H4 Neandertal/Middle Paleolithic combined results, and is therefore confined to the southern half of the distribution of suitable habitat for early modern humans (EMHs) for the H4. Prominent areas of overlapping habitat suitability include the Ebro River Valley, scattered areas throughout the Iberian Peninsula, southern France, the Apennine Peninsula, the Great Hungarian Plain, the Dnieper Uplands, the lowland areas south of the Carpathian Mountains, the Balkan Peninsula, the Anatolian Peninsula, and a few pixels scattered across the major Mediterranean islands. No overlap in suitable habitat is identified north of the Alps during the H4.

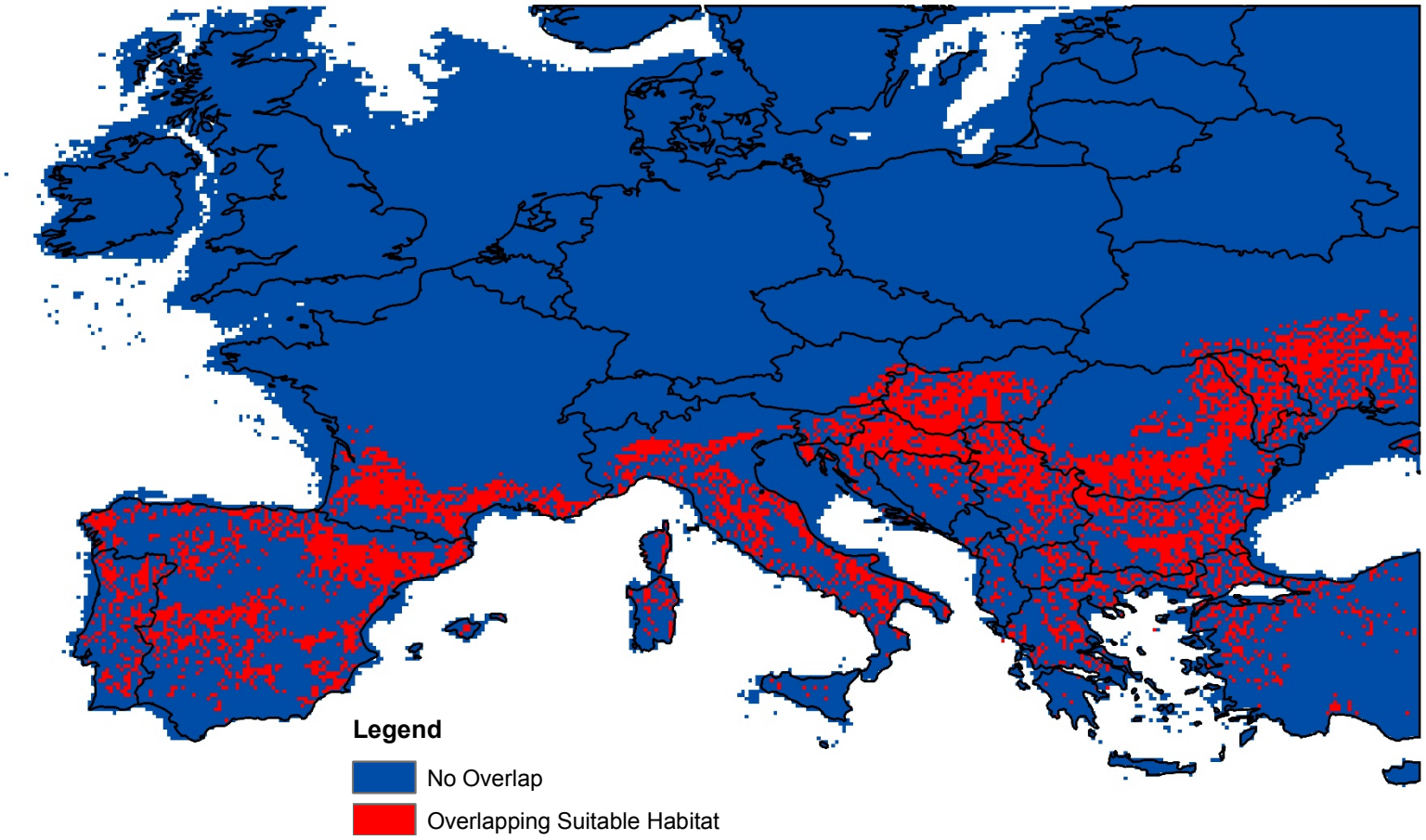

Figure 59. Geographic overlap between majority predictions of H4 Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive models.

6.4.3 Post-H4 Overlap

The smallest amount of geographic overlap for Neandertal/Middle Paleolithic combined consensus models and Upper Paleolithic consensus models occurs during the Post-H4. This overlap is illustrated in Figure 60. The geographic area predicted present for suitable habitat in both models consists of 9% percent of the total study area or 5,335 pixels. This area covers 39% of the Neandertal/Middle Paleolithic combined majority consensus prediction and only 33% of the Upper Paleolithic exclusive. The overall extent of the overlap drops by only 2% during the Post-H4 from the previous time period (the H4). The overall drop from the Pre-H4 to Post-H4 is 13% of the total study area.

As with the H4, the northern and southern latitudinal bounds of the overlap match that of the Post-H4 Neandertal/Middle Paleolithic combined results, and is therefore confined to the southern half of the distribution of suitable habitat for early modern humans (EMHs) during the Post-H4. Prominent areas of overlapping habitat suitability include the Ebro River Valley, northwestern and central Iberian, southern France, the Mediterranean coastline of France, the Apennine Peninsula south of the Alps, the Great Hungarian Plain, the eastern Danube River Valley, the Balkan Peninsula, the Anatolian Peninsula, and a few pixels on Sardinia and Corsica. No overlap is identified north of the Alps during the Post-H4. It should be noted that there are major areas of overlap identified both north and south of the Ebro River Valley.

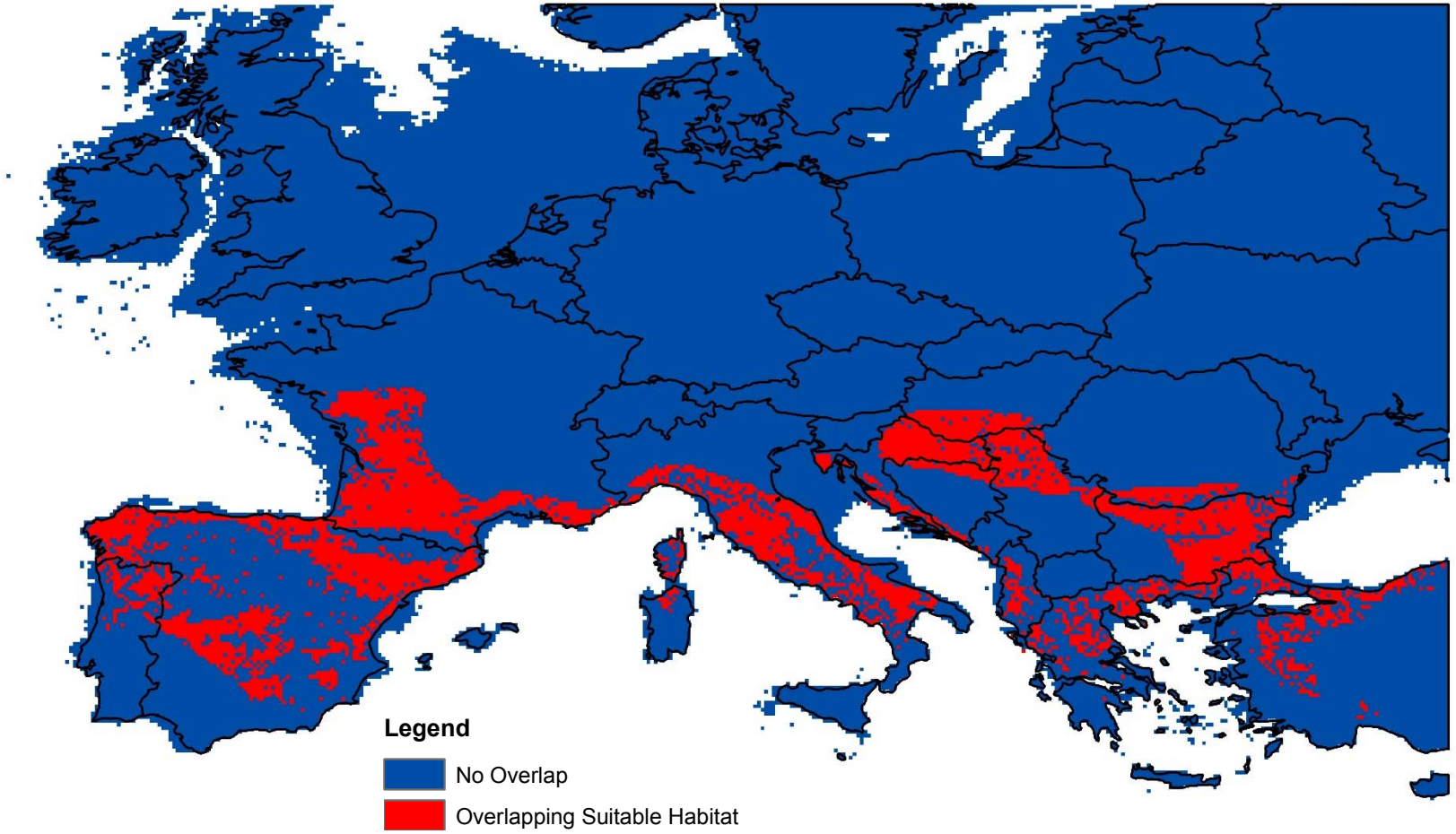

Figure 60. Geographic overlap of the majority consensus prediction maps for both the combined Neandertal fossil/Middle Paleolithic combined and Upper Paleolithic exclusive samples during the Post-H4.

7. DISCUSSION

This dissertation investigated the significance of the patterning and geographic distributions of Late Neandertals, early modern humans (EMHs), and their associated technocomplexes in Europe during the Late Pleistocene (43.3 – 36.5 ky cal BP) using ecological niche model (ENM) methods. This time period is of great interest in understanding Neandertal extinction, the expansion of EMHs in Europe, the Late Pleistocene population dynamic of hominins between those two groups, the end of the European Middle Paleolithic, and the origins of the European Upper Paleolithic. This dissertation focused on examining the potential distribution of late surviving European Neandertals and EMHs via reconstructions of the extent of the suitable habitat associated with those populations during the Pre-H4 (43.3 – 40.2 ky cal BP), H4 (40.2 – 38.6 ky cal BP), and the Post-H4 (38.6 – 36.5 ky cal BP) paleoenvironmental reconstructions (Banks et al. 2008b).

This section discusses the major implications of this dissertation's results, including the major temporal and geographic trends for the different types of consensus prediction models and overlap analysis between the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive samples. In addition, this section covers what these results imply for the Ebro Frontier Model (EFM) and its appropriateness as a theoretical model of hominin population dynamics of Late Pleistocene Iberia.

7.1 Limitations of This Study

There are limitations that this analysis encountered that have the potential to impact the results and thus should be addressed here. These center on sample design and issues pertaining to both the availability of the data and the choices of the author as to which of the available data to include in the study. The absolute size of the datasets available to both paleoanthropologists and Paleolithic archaeologists tend to be quite small in comparison with other fields. Paleo-studies in anthropology are limited to what has been preserved and discovered in the fossil record. European and Neandertal studies have enjoyed the benefit of intense study by paleoanthropologists and archaeologists, though this comes at the high cost of Eurocentrism in both analysis and interpretation.

These results are viewed through two lenses: 1) the current state of the archaeological and fossil record and, 2) which material of those records that has been absolutely dated. While both of these sample choice criteria reduce the absolute number of sites available to this dissertation, the second was put in place to ensure that all sites used to build the predictive models dated to the correct paleoenvironmental reconstructions. This more conservative view of where Neandertals and EMHs were located across Europe during the Pre-H4, H4, and Post-H4 was taken to prevent the inclusion of misclassified sites into the analysis. Thus, one limitation on sample design is inherent to the record from which the presence-points are drawn and the other is a self-imposed limitation of the study that was designed to see past the problems introduced by accidentally including sites which actually fall outside of the temporal subdivisions of this study.

7.2 The Patterning of Hominin Niche Predictions in Late Pleistocene Europe

Several major trends and implications become apparent when examining the results reported in Section 6. There is a distinct difference in the pattern of predicted areas of suitable habitat between samples representing Late Neandertals versus those representing early modern humans (EMHs) across the three paleoenvironmental time periods of this study. The patterns identified by these results have large-scale implications for our understanding of the process of Neandertal extinction and EMH expansion in Late Pleistocene Europe.

The results reported and discussed here do not falsify any of the major evolutionary models pertaining to Neandertal and EMH interaction in Europe during the Late Pleistocene, namely Recent African Origin (RAO), Afro-European Sapiens/African Hybridization and Replacement (AES/AHR), Assimilation Model (AM), and multiregional evolution (MRE). In fact, the results can be explained adequately under each of the different evolutionary models. Under RAO, however, these results would need to have a disclaimer whereby even if the two populations met, they were prevented from admixing by either biological inability or choice. This is perhaps not the most parsimonious explanation of the results, but they are still understandable with RAO. For both AES/AHR and AM, these results are easily interpreted as fitting very well with both of those models' predictions for Neandertal/EMH interaction. Under MRE, the results reported here also align with the predictions expected under the tenets of the model, especially in later formations of the model proposed in the literature. The original

MRE theoretical framework created in the 1980s and its predictions of Late Pleistocene population dynamics in Europe does not align with these results as well as with AM and AES/AHR, but they still do not falsify the model.

7.2.1 The Importance of the H4 and Post-H4

The pattern of the total area predicted as present for suitable habitat with the Neandertal exclusive, Neandertal/Middle Paleolithic combined, Upper Paleolithic exclusive, and the overlap analysis changes throughout the three time periods covered by this study. The consensus models meant to examine Neandertal range show large-scale contractions during the H4. This result is not unsurprising given the nature of the brutal cold and violent climatic fluctuations that characterize this time period in comparison to the previous warmer interstadial period of the Pre-H4 (Huijzer and Isarin 1997).

However, despite the fact that the temperatures grew somewhat warmer and were characterized by less dramatic fluctuations during the Post-H4 (Van Andel and Tzedakis 1996), the range of Neandertal suitable habitat did not recover to the levels shown during the Pre-H4. The total number of pixels predicted present only increases slightly in the Post-H4 from the preceding H4. This pattern is seen in both the trends in the majority and minimum consensus prediction maps. Based on these results, the importance of the H4 for Neandertal extinction cannot be overstated. This period of climatic upheaval is identified as the beginning of the extinction event for this population.

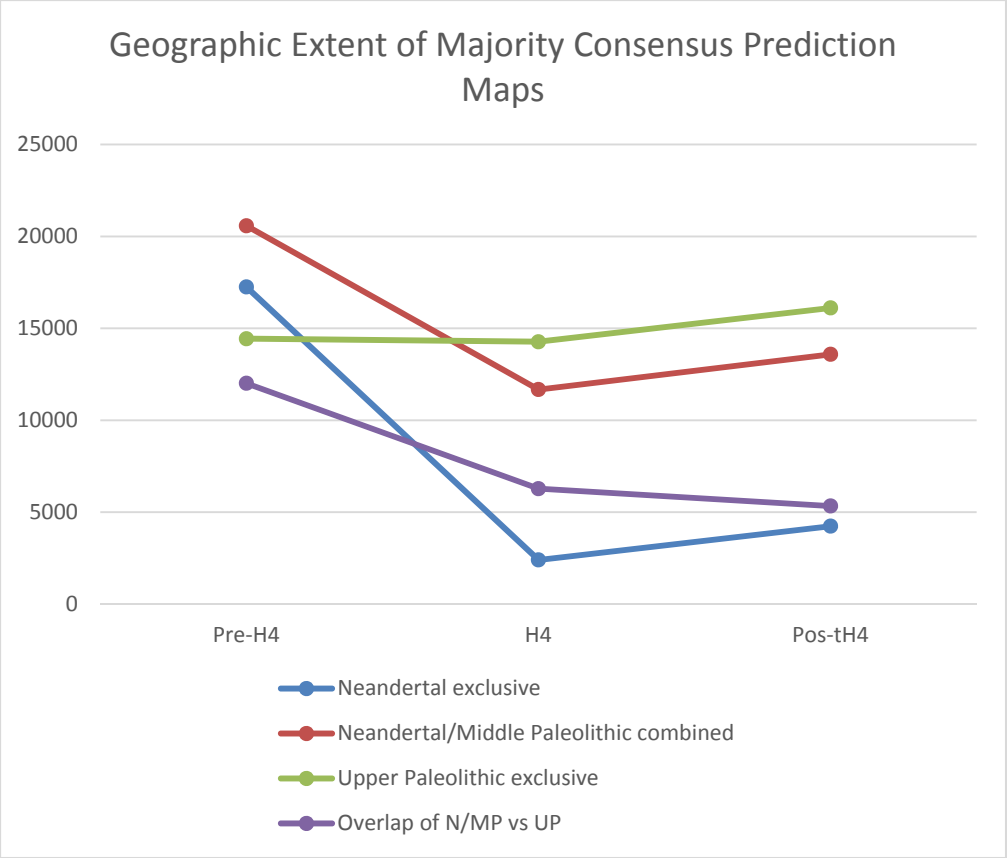

Figure 61. Trends in pixels counts of the majority consensus prediction maps for the Neandertal exclusive, Neandertal/Middle Paleolithic combined, Upper Paleolithic exclusive, and overlap of the N/MP vs. UP.

The amount of overlap between majority consensus prediction maps of the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive samples through time also reduces sharply in the H4 and slightly further still in the Post-H4 (Figure 61). This result is in contrast to the slight uptick of total area predicted present seen for the Neandertal exclusive and Neandertal/Middle Paleolithic combined samples across the three paleoenvironmental reconstructions. This is an important result when combined with the results of the other consensus prediction models, as it indicates that,

even though there was a slight recovery for Neandertals during the Post-H4, the potential area of contact for Late Neandertals and EMHs shows a progressive constriction through time.

While the H4 appears to be the significant turning point for Late Neandertals, for EMHs the Post-H4 majority consensus prediction maps of the Upper Paleolithic exclusive samples shows the first increase in total area of suitable habitat. The Upper Paleolithic consensus models, which are meant to model the EMH range, remain steady from the Pre-H4 to the H4 with only a 1% reduction in total area between the two time periods. There is a 4% increase between the H4 to Post-H4 on the majority maps. This pattern is not as dramatic as the changes shown for the Neandertal exclusive and Neandertal/Middle Paleolithic combined samples and, when examining the results of the minimum consensus prediction maps (Figure 62), the uptick during the Post-H4 disappears.

The major implication for the above results is that, despite the extreme climatic fluctuations and colder temperatures of the H4 (Huijzer and Isarin 1997), the extent of the EMH suitable habitat (and thus the distribution of this population) was unaffected. This is in direct contrast to the results shown for the Late Neandertals. There could be many different reasons for this difference in response to the H4, but one of the most interesting is behavioral. Archaeological and paleoanthropological research has focused for many years on identifying the differences, or lack thereof, between Neandertal and EMH patterns, not only in the types of stone tools that make up the technocomplexes made by each group (Carbonell et al. 2000; Golovanova et al. 2010; Maroto et al. 1996;

Maroto et al. 2012; Wood et al. 2014), but also in behavior with hunting strategies (Berger and Trinkaus 1995; Schmitt et al. 2003), clothing (Shipman 2008), and mobility patterns (Shaw and Stock 2013; Trinkaus 1993), etc.

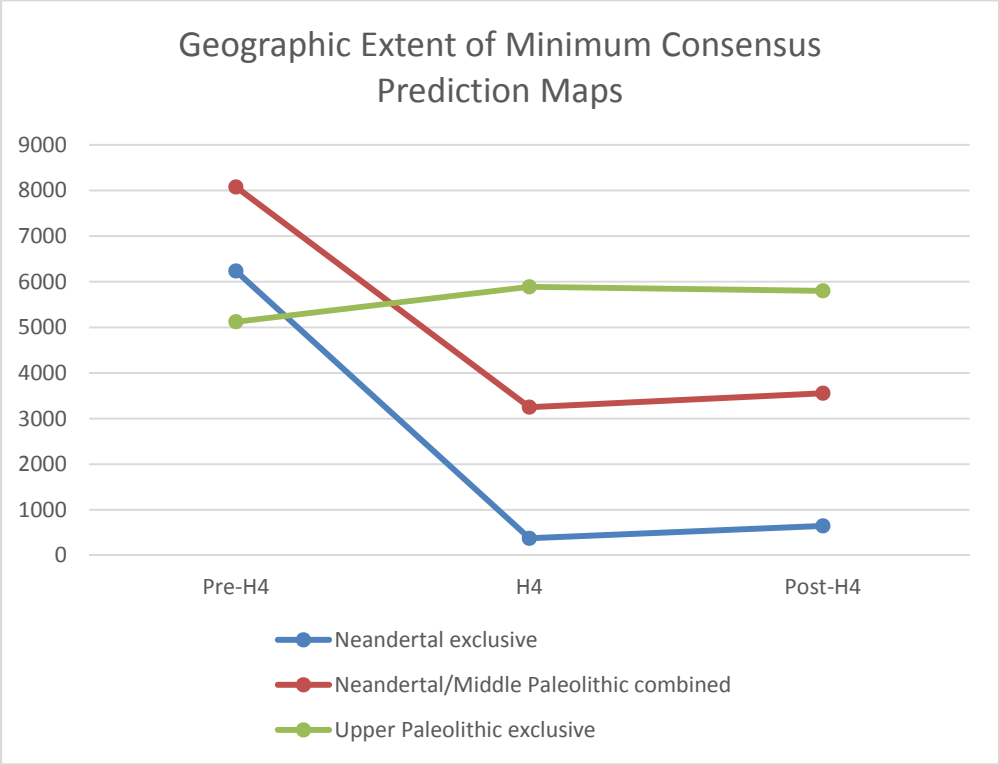

Figure 62. Trends in pixels counts of the minimum consensus prediction maps for the Neandertal exclusive, Neandertal/Middle Paleolithic combined, and the Upper Paleolithic exclusive.

This dissertation cannot conclude what differences led to the trends shown here, but it does show that there were distinct differences in total geographic extent of the suitable habitat for Neandertals and EMHs from 43.3 to 36.5 ky cal BP, which implies a difference in the deliberate behaviors concerning site-choice. The geographic extent of

the suitable habitat predicted for EMHs, based on the habitat where we know they were located across Europe, covered a larger total proportion of the total study area and was found in more northern regions than was found for Neandertals during the H4 and Post-H4. The results of this dissertation indicate that different behavioral patterns allowed EMHs to inhabit a larger area during the H4 and Post-H4 than did Neandertals.

7.2.2 Difference in Patterning of Suitable Habitat in and around Mountain Ranges

Patterns of Neandertal and early modern human (EMH) behavior in regards to mountain ranges becomes apparent when the majority and minimum consensus prediction maps are examined. Those behaviors, reconstructed via a conservative sample of presence-points from the fossil and archaeological records, show that both groups likely avoided the Alps during all three paleoenvironmental reconstructions. This high, glaciated mountain range consistently lacks the presence of suitable habitat for all of the different experimental designs and sample types used in this study. The Pyrenees also are consistently predicted as absent for both Late Neandertals and EMHs. This result is not surprising considering that the Alps and the Pyrenees are the two mountain ranges in the study area with the highest overall average elevation and would have experienced glaciation to varying degrees throughout the study period (Turu et al. 2016; Van Andel and Tzedakis 1996).

For the four models created to investigate Neandertal patterns, the mountain ranges of Europe that have lower average elevations than the Alps and the Pyrenees show inclusions of suitable habitat within their borders on the majority maps. These

include the Carpathians, the Balkans, the Dinaric Alps, the Pindus, the Apennines, and the high rugged areas of the Massif Central and Meseta Central. However, the EMHs reconstructed range of suitable habitat on the majority maps typically show less presence within the main bodies of those mountain ranges. This pattern of Neandertal suitable habitat being found more often in mountainous areas is not solely due to the elevation of the areas, but the interaction between all 8 layers in the paleoenvironmental reconstructions (described in Section 4.1).

7.2.3 Suitable Habitat Presence on Major Mediterranean Islands

The consensus prediction models, along with their majority, minimum, and maximum prediction maps, are hypotheses that reconstruct the physical location of habitat similar to the samples used to generate the models. These methods will identify suitable habitat in areas where we have either not yet found hominin presence, or, geographic areas which actually fell outside of the range of Late Neandertals and EMHs. Some areas of interest to this discussion include the major islands of the Mediterranean which fall inside the study area: Sicily, Sardinia, Corsica, Ibiza, Mallorca, and Menorca.

Neandertal presence has yet to be documented on any of these islands, but suitable habitat is found in even the minimum prediction maps for all except the Pre-H4 Middle Paleolithic exclusive consensus prediction model, which excluded sites where Neandertal fossils have been found. All models that include Neandertal fossil locations also include some level of identified habitat similarity on one or more of the major Mediterranean islands. This geographic pattern is similar to the results of the Upper

Paleolithic exclusive models and the overlap analysis comparing the majority maps for the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive models.

These results indicate that if Neandertals and EMHs could access those areas, then they would have been able to exist on those islands. Currently, Sardinia is the only one of the islands with a published record detailing a hominin fossil record that extends past the late Neolithic. A portion of a proximal modern human phalanx was discovered in 1993 at Corbeddu Cave on the island of Sardinia and is dated to approximately 20,000 years BP (Sondaar et al. 1995). This find, combined with the results of this dissertation, indicate that the hominin occupation of Sardinia and Corsica, which were not connected to mainland Italy even during the Last Glacial Maximum, is likely much deeper than has been previously thought.

7.2.4 Trends in the Overlap between Neandertal/Middle Paleolithic and Upper Paleolithic Exclusive Majority Consensus Prediction Maps

The results of the overlap analyses reported here indicate that there was an overall trend from the Pre-H4 to Post-H4 of more to less extensive opportunity for contact between Neandertals and the makers of the Upper Paleolithic technocomplexes, assumed to be EMHs. The area of overlap shown on the majority consensus prediction maps for the Neandertal/Middle Paleolithic combined and Upper Paleolithic exclusive samples drops most dramatically from the Pre-H4 to H4 with a shallower drop in overlap from the H4 to Post-H4. During the H4 and Post-H4, the areas identified as having similar habitat suitability values for both groups are largely confined to southern Europe.

This is caused by the latitudinal restriction of the Neandertal range that occurs during these periods.

All results of the overlap analysis show the Ebro River Valley as an area where there is a high concentration of habitat suitable to both Neandertals and EMHs. This indicates that the Ebro River Valley was unlikely to have been an impermeable biogeographic barrier to hominins. These results also show areas of overlap both south and north of this valley during the Pre-H4, H4, and Post-H4. The Pyrenees Mountains appear as the most significant area of absence blocking the entrance and exit of the Iberian Peninsula. The areas described in Section 6.4 indicate places where it is highly likely that Neandertals and EMHs came into contact with one another.

Rather than splitting the Middle Paleolithic and Upper Paleolithic stone tool technologies into smaller subcategories such as Mousterian, Châtelperronian, Uluzzian, Bohunician, etc., this project combined them under the umbrella of either Middle Paleolithic or Upper Paleolithic. This was to aid in investigating questions pertaining to large-scale population level differences of Neandertals and modern humans, rather than examining the differences in ranges of sub-populations of EMHs *or* late surviving Neandertals. Research questions examining sub-populational differences such as Solutrean vs. Epigravettian are interesting and pertinent in their own right, but were not the aim of this research.

The trend for reduced geographic opportunity of populational contact can be explained by shrinking Neandertal population sizes and thus reduced presence on the landscape as they underwent the process of extinction. As Neandertals went extinct, it is

expected that the sample sizes available to this type of research would also shrink. How that process occurred, by competition or assimilation, is still under debate and this research does not seek to answer those questions.

7.3 The Ability of Middle Paleolithic Calibrated Models to Predict Sites with Diagnostic Neandertal Fossils

As a secondary goal, this project sought to test the major theoretical assumption that Middle Paleolithic sites can be assumed to stand as proxy for Neandertal presence. In order to quantify this assumption so it could be objectively investigated, predictive models were created using samples of absolutely dated Middle Paleolithic sites for the Pre-H4, H4, and Post-H4 paleoenvironmental reconstructions. These models were then tested to see if they could predict discrete samples of sites that have produced Neandertal remains dated to the same periods at a better than random rate (the alternative hypothesis). The null hypothesis states that the Middle Paleolithic models could not predict Neandertal sites at a better than random rate.

The results of this project indicate that the assumption that Middle Paleolithic archaeological sites can stand as proxies for Neandertal presence is ***not*** appropriate for all time periods and places. Here, one of the three models, the Pre-H4 MP calibrated model, produced mixed results. That consensus prediction model generated thresholded results that yielded a marginally significant *p*-value using cumulative binomial probabilities, but the Partial-ROC score based on the unthresholded results did not perform as well statistically. However, the H4 and Post-H4 Middle Paleolithic calibrated

models were able to predict test points at a better than random rate using both cumulative binomial probabilities and Partial-ROC tests. This method of testing offers a novel approach to investigating questions concerning the validity of the very common theoretical assumption regarding the nature of archaeological cultures and hominin populations. It is not yet clear how much decreasing calibration and validation sample sizes impacts the statistical significance of the results. As these sample sizes reduce, test results get increasingly more significant. Future work, as discussed in Section 7.5, will include experiments specifically designed to investigate the impacts of smaller sample sizes on these types of tests.

7.4 The Neandertal Exclusive Models and Sample Size

This project also tested whether or not samples of absolutely dated locations with Neandertal remains could produce coherent and statistically significant models. Each of these three experiments were produced with the *n*-1 testing and validation procedures. The experiments for the Neandertal exclusive samples for the Pre-H4 and H4 both resulted in models that were able to predict eliminated test points at a better than random rate. The Pre-H4 resulted in a *p*-value of 0.0006 and the H4 a *p* of 0.02. However, the Neandertal exclusive model for the Post-H4 resulted in a *p* of 0.35 on run 1 of the experiment and 0.06 from run 2. The Post-H4 experiments never reached values that could be considered truly indicative of creating models that, beyond a doubt, predict Neandertal test sites at a better than random rate. This is most likely due to the extremely small sample sizes in the Post-H4.

This study is bound by the constraints of the fossil record and, as Neandertals moved closer to extinction, we would expect to see fewer sites producing diagnostic fossil remains of this population. Thus, there is a reducing trend throughout the three study periods of the algorithm to create models of Neandertal fossil locations that predict test points at a better than random rate. This trend is a result of both reducing sample size and the nature of the fossil record at the time.

7.5 The Implications of These Results for the Ebro Frontier Model (EFM)

The results of this dissertation have implications for the Ebro Frontier Model (EFM) and its use as a hypothetical model of Neandertal extinction and early modern human (EMH) expansion on the Iberian Peninsula. The interpretation of the majority consensus prediction maps reported in Section 6 produce a balanced picture of the consensus models that is more conservative than the maximum, but less conservative than the highly restrictive minimum maps. The majority maps identify the presence of suitable habitat if a majority of the thresholded replicates used to build the consensus model agree on that prediction of presence. The minimum maps do offer important information on the exact location of pixels where all replicates are in agreement, but often create a graphic illustration of that geographic extent that is quite small.

The majority maps for the Upper Paleolithic exclusive sample during the Pre-H4, H4, and Post-H4 all identify large areas of suitable habitat for EMHs south, north, and within the Ebro River Valley. This conclusion runs counter to the hypotheses put forth in the published literature describing the tenets of the EFM (Zilhão 2000; Zilhão 2009).

There was no ecological reason preventing Late Neandertals and EMHs from occupying areas south of the Ebro River Valley prior to the date of 30,000 years BP. In fact, the largest amount of overlapping areas of suitable habitat between the two populations occurred during the Pre-H4, well before the dates hypothesized by the EFM. In other words, if EMHs were able to access the area of the Iberian Peninsula south of the Ebro River Valley, their behavioral choices as established by multiple Upper Paleolithic localities throughout western and central Europe would have facilitated contact between the two populations.

Even the highly conservative minimum maps indicate the presence of suitable habitat for both groups north and south of the Ebro River Valley, though these maps show more concentrated areas of suitable habitat for both Neandertals and EMHs within the Ebro River Valley and north of that point. The EFM not only hypothesizes that EMHs were confined to the northern extremes of the Iberian Peninsula, it also states that Neandertals were confined to the area south of the Ebro River Valley prior to the dissolution of the frontier. These results indicate that there was no ecological reason to assume that Neandertals would have been confined to southern Iberia.

The pattern of overlap on the Iberian Peninsula and habitat that was available to both Neandertals and EMHs fluctuated between the Pre-H4, H4, and Post-H4. This reflects the fluctuating climate from 43.3 – 36.5 ky cal BP as modeled by Banks and colleagues (2008b). The climate during the time period of this study was never what one could deem “stable” (Huijzer and Isarin 1997; Turu et al. 2016; Van Andel and Tzedakis 1996) and a barrier or frontier created by habitat differences (Zilhão 2009) would also

fluctuate across geographic space to reflect those climatic changes. If an ecological or biogeographic frontier existed, it would have moved north, or disappeared from Iberia entirely, during the warmer periods of the Pre-H4 and Post-H4. During colder periods, such as the H4, this hypothetical frontier would have moved farther south on the peninsula. During the H4, which was characterized by violent and quick climatic fluctuations (Huijzer and Isarin 1997; Turu et al. 2016), this frontier could have moved with relative rapidity north and south across the Iberian Peninsula, likely at different rates and at different times.

The only features that would have prevented large-scale movement of hominins and remained stationary on the landscape were the extremely high mountain ranges of the Alps and Pyrenees. The Pyrenees Mountains are especially pertinent to this discussion, as they have the potential to limit movement by hominins both into and out of Iberia. The pattern of glacial advance and retreat across the entirety of the Pyrenees was a complicated one and the glaciers found there during the time period of this study were not distributed evenly across the mountain range. The presence and extent of the glaciers would advance and retreat with the fluctuating climate (Turu et al. 2016). The results of this dissertation indicate that the Pyrenees Mountains lacked habitat suitable for Neandertals and EMHs during the period of this study. The patterns seen here indicate that the behavioral choices of these two groups would have confined full-scale occupation and site-choice to the areas of lower elevation on the west and east of this mountain range.

The results of this dissertation indicate that, if a biogeographic frontier existed on the Iberian Peninsula, we must further investigate the intricacies of the patterns of the Neandertal and EMH behavior, population dynamics, and suitable habitat in reference to a constantly changing climate in order to refine our understanding of where that barrier would have been located at different times. The pattern of Neandertal extinction, EMH expansion, and the population dynamics between the two groups as illustrated here demonstrates the complicated nature of the mode and tempo of these interacting processes. This dissertation adds to the conversation on Neandertal extinction and EMH expansion by using a novel method to investigate these patterns and their fluctuation over time.

8. CONCLUSIONS

This dissertation sought to investigate the opportunity that Late Neandertals and early modern humans (EMHs) may have had for contact on the European landscape prior to Neandertal extinction. The results generated show that Neandertal and EMH suitable habitat, an approximation of their fundamental niche parameters, overlapped for the entirety of the temporal period of the Pre-H4 (43.3 – 40.2 ky cal BP), the H4 (40.2 – 38.6 ky cal BP), and the Post-H4 (38.6 – 36.5 ky cal BP) in multiple geographic regions across Europe, despite the different behavioral patterns apparent in their response to fluctuating climate. There was no ecological reason preventing contact between Neandertals and EMHs in Europe from 43.3 to 36.5 ky cal BP in at least some geographic areas. Given the large amount of geographic overlap seen here, it is highly unlikely that the two populations never came into contact with one another during the study period.

Using ecological niche modeling (ENM) methods, the Genetic Algorithm for Rule-Set Prediction (GARP) specifically, allowed this study to model the extent of the suitable habitat for Late Neandertals and EMHs in western and central Europe. Since the reconstruction of these areas of predicted presence for suitable habitat are based on the habitat associated with known locations of Neandertals and EMHs, this dissertation ultimately is able to begin to address the difference in patterns of behavior on the landscape for these two populations. The sample of locations representing Late Pleistocene hominins portrays deliberate behaviors concerning site-choice during the

time periods of three paleoenvironmental reconstructions representing a fluctuating climate, as viewed through the lenses of the current state of the archaeological record and the availability of absolute dating on those sites.

While models of Neandertal and EMH suitable habitat indicate large amounts of geographic overlap for these two groups, there were different patterns between the two groups that emerged during the course of this study. During the H4, the geographic extent of Neandertal suitable habitat shows large-scale contraction and latitudinal restriction to southern Europe. It does not recover to its Pre-H4 levels during the Post-H4. In contrast, the geographic extent of suitable habitat for EMHs does not contract during the H4, but remains steady from the Pre-H4 to H4 and increases slightly in the Post-H4. The behavioral patterns of these two groups shown here indicate that the cold, glacial period of the H4 did not affect EMH patterns of site-choice in the same manner as it did Neandertals.

This research demonstrated the importance of investigating questions regarding Late Pleistocene population dynamics in Europe, even though there are theoretical and methodological limitations on paleoanthropological research in general and this dissertation in particular. Late Neandertal and EMH populations possessed fundamental niche parameters and patterns of behavior that were similar enough to allow for large amounts of geographic overlap throughout the Pre-H4, H4, and Post-H4. This geographic overlap can be speculated to indicate that there was ample opportunity for the two populations to come into contact with one another and experience admixture, competition, or a combination of both. The fluctuation in the extent and continuity of

both the overlap and individual niche parameters over the course of the three environmental reconstructions used here demonstrates that Late Pleistocene population dynamics in Europe were complex.

This project also addressed secondary questions concerning the predictive ability of consensus models calibrated with archaeological sites and tasked with predicting the locations of hominin fossils. The results of models made with Middle Paleolithic archaeological sites and their ability to correctly classify Neandertal fossil locations show that the statistical ability of archaeologically based models to predict fossil locations varies throughout time. The implication from this conclusion is that the one-to-one correlation between archaeological technocomplexes and biological populations cannot always be taken for granted. Future work will include more detailed investigations concerning this topic.

Additional studies will help to further our understanding of the population dynamics occurring between Neandertals and early modern humans (EMHs) during the Late Pleistocene beyond the current scope of these results. Future research will expand the geographic and temporal scope of the paleoenvironmental reconstructions used in this dissertation. This will allow the comparison of the patterns seen here to other climatic events, such as Heinrich Events, stadials, and interstadial events that precede and follow the time range of this study. Questions concerning the way that Neandertals react to other climatic events prior to EMH appearance in Europe, how that compares with these results, and how EMHs might be affecting Neandertal behavior and response to climatic fluctuations could then be addressed.

REFERENCES

Adjemian JC, Girvetz EH, Beckett L, and Foley JE. 2006. Analysis of Genetic Algorithm for Rule-Set Production (GARP) modeling approach for predicting distributions of fleas implicated as vectors of plague, Yersinia pestis, in California. Journal of medical entomology 43(1):93-103.

Aiello LC. 1993. The fossil evidence for modern human origins in Africa: a revised view. American Anthropologist 95(1):73-96.

Anderson RP, Gómez-Laverde M, and Peterson AT. 2002. Geographical distributions of spiny pocket mice in South America: insights from predictive models. Global Ecology and Biogeography 11(2):131-141.

Anderson RP, Lew D, and Peterson AT. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological modelling 162(3):211-232.

Angelucci DE, and Zilhão J. 2009. Stratigraphy and formation processes of the Upper Pleistocene deposit at Gruta da Oliveira, Almonda karstic system, Torres Novas, Portugal. Geoarchaeology 24(3):277-310.

Anikovich MV, Sinitsyn AA, Hoffecker JF, Holliday VT, Popov V, Lisitsyn S, Forman SL, Levkovskaya G, Pospelova G, and Kuz'Mina I. 2007. Early Upper Paleolithic in Eastern Europe and implications for the dispersal of modern humans. Science 315(5809):223-226.

Antunes N, Banks W, and D'Errico F. 2014. Evaluating Viking eco-cultural niche variability between the Medieval Climate Optimum and the Little Ice Age: a feasibility study. Debating Spatial Archaeology. p 113-130.

Aparicio Pérez J. 2014. Cova Foradà (Oliva. Valencia). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 356-361.

Aparicio Pérez J, Subirà de Galdàcano E, Gómez Merino G, Lorenzo C, Lozano M, and Herrero Cortell M. 2014. Los Neandertales de la Cova Foradà de Oliva. (Estado actual de la investigación). In: Valenciana RAdC, editor. Sección de Estudios Arqueológicos y Prehistóricos. Valencia: Real Acadèmia de Cultura Valenciana.

Ardèvol JR, and Salomó AC. 2014. Las Fuentes de San Cristóbal (Veracruz, Huesca). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and

the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 179-181.

Baena J, Carrión E, Cuartero F, and Fluck H. 2012. A chronicle of crisis: the Late Mousterian in north Iberia (Cueva del Esquilleu, Cantabria, Spain). Quaternary International 247:199-211.

Baena Preysler J, and Carrion Santafé E. 2014. Cueva de El Esquilleu: a new point of reference for the Cantabrian Mousterian. In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 82-87.

Banks WE. 2015. Constructing chronologies for the late Middle Paleolithic and Upper Paleolithic: limitations and means to overcome them. World Archaeology 47(4):585-600.

Banks WE, Aubry T, d'Errico F, Zilhão J, Lira-Noriega A, and Peterson AT. 2011. Eco-cultural niches of the Badegoulian: unraveling links between cultural adaptation and ecology during the Last Glacial Maximum in France. Journal of Anthropological Archaeology 30(3):359-374.

Banks WE, d'Errico F, Peterson AT, Kageyama M, and Colombeau G. 2008a. Reconstructing ecological niches and geographic distributions of caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*) during the Last Glacial Maximum. Quaternary Science Reviews 27(27):2568-2575.

Banks WE, d'Errico F, Peterson AT, Kageyama M, Sima A, and Sánchez-Goñi M-F. 2008b. Neanderthal extinction by competitive exclusion. PLoS One 3(12):e3972.

Banks WE, d'Errico F, Peterson AT, Vanhaeren M, Kageyama M, Sepulchre P, Ramstein G, Jost A, and Lunt D. 2008c. Human ecological niches and ranges during the LGM in Europe derived from an application of eco-cultural niche modeling. Journal of Archaeological Science 35(2):481-491.

Banks WE, d'Errico F, and Zilhão J. 2013a. Human–climate interaction during the Early Upper Paleolithic: testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian. Journal of human evolution.

Banks WE, d'Errico F, Dibble HL, Krishtalka L, West D, Olszewski DI, Peterson AT, Anderson DG, Gillam J, and Montet-White A. 2006. Eco-cultural niche modeling: new tools for reconstructing the geography and ecology of past human populations. PaleoAnthropology 4:68-83.

Banks WE, d'Errico F, and Zilhão J. 2013b. Revisiting the chronology of the Proto-Aurignacian and the Early Aurignacian in Europe: A reply to Higham et al.'s comments on. Journal of human evolution 30:1e8.

Banks WE, Zilhão J, d'Errico F, Kageyama M, Sima A, and Ronchitelli A. 2009. Investigating links between ecology and bifacial tool types in Western Europe during the Last Glacial Maximum. Journal of Archaeological Science 36(12):2853-2867.

Bar-Yosef O, and Belfer-Cohen A. 2001. From Africa to Eurasia—early dispersals. Quaternary International 75(1):19-28.

Barroso C, Caparrós M, Barsky D, Moigne AM, and Monclova A. 2014. Boquete de Zafarraya cave: A Neanderthal site in southern Iberia. In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 463-472.

Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J, and Villalobos F. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling 222(11):1810-1819.

Beauval C, Lacrampe-Cuyaubère F, Maureille B, and Trinkaus E. 2006. Direct radiocarbon dating and stable isotopes of the Neandertal femur from Les Rochers-de-Villeneuve (Lussac-les-Châteaux, Vienne). Bulletins et Memoires de la Societe d'Anthropologie de Paris(18 (1-2)):35-42.

Berger TD, and Trinkaus E. 1995. Patterns of trauma among the Neandertals. Journal of Archaeological Science 22(6):841-852.

Bertranpetit J, and Cavalli-Sforza LL. 1991. A genetic reconstruction of the history of the population of the Iberian Peninsula. Annals of human genetics 55(1):51-67.

Bischoff JL, Shamp DD, Aramburu A, Arsuaga JL, Carbonell E, and De Castro JB. 2003. The Sima de los Huesos Hominids date to beyond U/Th equilibrium (> 350kyr) and perhaps to 400–500kyr: New radiometric dates. Journal of Archaeological Science 30(3):275-280.

Bocherens H, Drucker DG, Billiou D, Patou-Mathis M, and Vandermeersch B. 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: review and use of a multi-source mixing model. Journal of human evolution 49(1):71-87.

Boule M. 1913. L'homme fossile de La Chapelle-aux-Saints: Masson.

Boule M. 1921. Les hommes fossiles: éléments de paléontologie humaine: Masson.

Boule M. 1923. Fossil Men: Elements of Human Palaeontology, trans. JE Ritchie and J Ritchie, Edinburgh: Oliver and Boyd.

Bower B. 1988. An Earlier Dawn for Modern Humans? Science News:138-138.

Brace CL. 1962. Refocusing on the Neanderthal problem. American Anthropologist 64(4):729-741.

Brace CL, Agogino GA, Brothwell DR, Clark WLG, Coon CS, Farmer MF, Genovés S, Givens RD, Howell FC, and Howells W. 1964. The Fate of the" Classic" Neanderthals: A Consideration of Hominid Catastrophism [and Comments and Reply]. Current Anthropology:3-43.

Bräuer G. 1984. The 'Afro-European sapiens hypothesis' and hominid evolution in East Asia during the Late Middle and Upper Pleistocene. Cour Forsch-Inst Senckenberg 69:145-165.

Bruner E, and Pearson O. 2013. Neurocranial evolution in modern humans: the case of Jebel Irhoud 1. Anthropological Science 121(1):31-41.

Burke A. 2004. The ecology of Neanderthals: preface. International Journal of Osteoarchaeology 14(3-4):155-161.

Burkitt MC. 1921. Prehistory: Univ of California Press.

Carbonell E, Vaquero M, Maroto J, Rando J, and Mallol C. 2000. A geographic perspective on the Middle to Upper Paleolithic transition in the Iberian Peninsula. The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean Peabody Museum Bulletin 8:5e34.

Cardoso JL. 2006. The Mousterian complex in Portugal. Zephyrvs 59:21-50.

Casanova J, Torcal RM, Gilabert XR, Martínez-Moreno J, Roy M, and Vega S. 2014. The Middle Paleolithic sequence of Cova de l'Estret de Tragó (Lleida, Pre-Pyrenees). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. p 167-170.

Cavalli-Sforza LL. 1966. Population structure and human evolution. Proceedings of the Royal Society of London Series B, Biological Sciences 164(995):362-379.

Cavalli-Sforza LL. 1998. The DNA revolution in population genetics. Trends in Genetics 14(2):60-65.

Cavalli-Sforza LL, and Edwards AW. 1967. Phylogenetic analysis. Models and estimation procedures. American journal of human genetics 19(3 Pt 1):233.

Cavalli-Sforza LL, Piazza A, Menozzi P, and Mountain J. 1988. Reconstruction of human evolution: bringing together genetic, archaeological, and linguistic data. Proceedings of the National Academy of Sciences 85(16):6002-6006.

Chase PG, Debénath A, Dibble HL, McPherron SP, Schwarcz HP, Stafford TW, and Tournepiche J-F. 2007. New dates for the fontechevade (Charente, France) homo remains. Journal of human evolution 52(2):217-221.

Chen G, and Peterson A. 1999. A new technique for predicting distribution of terrestrial vertebrates using inferential modeling. Zoological research/" Dong wu xue yan jiu" bian ji wei yuan hui bian ji 21(3):231-237.

Chen P, and Arratia G. 2010. Oldest known Mylopharyngodon (Teleostei: Cyprinidae) from the Mongolian Plateau and its biogeographical implications based on ecological niche modeling. Journal of Vertebrate Paleontology 30(2):333-340.

Churchill SE. 2014. Thin on the ground: Neandertal biology, archeology and ecology: John Wiley & Sons.

Churchill SE, and Smith FH. 2000. Makers of the early Aurignacian of Europe. American journal of physical anthropology 113(s 31):61-115.

Clark WLG. 1955. The fossil evidence for human evolution. Chicago: University of Chicago Press.

Condemi S, Mounier A, Giunti P, Lari M, Caramelli D, and Longo L. 2013. Possible Interbreeding in Late Italian Neanderthals? New Data from the Mezzena Jaw (Monti Lessini, Verona, Italy). PloS one 8(3):e59781.

Coon CS. 1962. The Origin of Races. New York: Alfred A Knopf.

Coon CS, Garn SM, and Birdsell JB. 1950. Races. A study of the problems of race formation in man Charles C Thomas, Springfield, IL:65-71.

Cortés-Sánchez M, Morales-Muñiz A, Simón-Vallejo MD, Lozano-Francisco MC, Vera-Peláez JL, Finlayson C, Rodríguez-Vidal J, Delgado-Huertas A, Jiménez-Espejo FJ, and Martínez-Ruiz F. 2011. Earliest known use of marine resources by Neanderthals. PloS one 6(9):e24026.

Cortés Sánchez M, and Simón Vallejo MD. 2014. Bajondillo cave (Toreemolinos, Malaga). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in

Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 430-434.

d'Errico F, and Banks WE. 2013. Identifying mechanisms behind Middle Paleolithic and Middle Stone Age cultural trajectories. Current Anthropology 54(S8):S371-S387.

d'Errico F, and Sánchez Goñi MaF. 2003. Neandertal extinction and the millennial scale climatic variability of OIS 3. Quaternary Science Reviews 22(8):769-788.

Danzeglocke U, Jöris O, and Werninger B. 2015. CalPal 2007–Radiocarbon Calibration Online.

Daura J, Sanz M, García N, Allué E, Vaquero M, Fierro E, Carrión J, López-García J, Blain H, and Sánchez-Marco A. 2013. Terrasses de la Riera dels Canyars (Gavà, Barcelona): the landscape of Heinrich Stadial 4 north of the "Ebro frontier" and implications for modern human dispersal into Iberia. Quaternary Science Reviews 60:26-48.

de la Rasilla M, Rosas A, Cañaveras JC, Lalueza-Fox C, Santamaría D, SánchezMoral S, Estalrrich A, Tabernero AG, Silva PG, Martínez E et al. . 2014. El Sidrón (Piloña, Asturias). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 122-128.

de Quiros FB, Campos AN, and Fernández JM. 2014. El Castillo Cave. In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 55-60.

De Torres T, Ortiz J, Grün R, Eggins S, Valladas H, Mercier N, TISNÉRAT-LABORDE N, Julià R, Soler V, and Martínez E. 2010. Dating of the Hominid (*Homo neanderthalensis*) Remains Accumulation from El Sidron Cave (Pilona, Asturias, North Spain): An Example of a Multi-Methodological Approach to the Dating of Upper Pleistocene Sites. Archaeometry 52(4):680-705.

Dobzhansky T. 1961. A bogus "science" of race prejudice. Journal of Heredity 52(4):189-190.

Dobzhansky T. 1963a. A debatable account of the origin of races. Scientific American 208(2):169-183.

Dobzhansky T. 1963b. Possibility that Homo sapiens evolved independently 5 times is vanishingly small. Current Anthropology 4(4):360-364.

Drell JR. 2000. Neanderthals: a history of interpretation. Oxford Journal of Archaeology 19(1):1-24.

Drucker D, and Bocherens H. 2004. Carbon and nitrogen stable isotopes as tracers of change in diet breadth during Middle and Upper Palaeolithic in Europe. International Journal of Osteoarchaeology 14(3-4):162-177.

Duarte C, Maurício J, Pettitt PB, Souto P, Trinkaus E, van der Plicht H, and Zilhão J. 1999. The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. Proceedings of the National Academy of Sciences 96(13):7604-7609.

Edwards AW, and Cavalli-Sforza LL. 1963. The reconstruction of evolution. Annals of Human Genetics 21(1):104-105.

Edwards AW, and Cavalli-Sforza LL. 1964. Reconstruction of evolutionary trees. In: Heywood W, and McNeill J, editors. Phenetic and Phylogenetic Classification. London: Systematics Association. p 67-76.

Estévez J. 2004. Vanishing carnivores: what can the disappearance of large carnivores tell us about the Neanderthal world? International Journal of Osteoarchaeology 14(3-4):190-200.

Finlayson C, Carrión J, Brown K, Finlayson G, Sánchez-Marco A, Fa D, Rodríguez-Vidal J, Fernández S, Fierro E, and Bernal-Gómez M. 2011. The< i> Homo</i> habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. Quaternary Science Reviews 30(11):1525-1532.

Finlayson C, Fa DA, Jiménez Espejo F, Carrión JS, Finlayson G, Giles Pacheco F, Rodríguez Vidal J, Stringer C, and Martínez Ruiz F. 2008. Gorham's Cave, Gibraltar—The persistence of a Neanderthal population. Quaternary International 181(1):64-71.

Finlayson C, Pacheco FG, Rodríguez-Vidal J, Fa DA, López JMG, Pérez AS, Finlayson G, Allue E, Preysler JB, and Cáceres I. 2006. Late survival of Neanderthals at the southernmost extreme of Europe. Nature 443(7113):850-853.

Foucher P, and Normand C. 2006. Etude de l'industrie lithique des niveaux solutréens de la grotte d'Isturitz (Isturitz/Saint-Martin-d'Arberoue, Pyrénées-atlantiques). Antiquités nationales 2004(36):199-216.

Fritz U, Fritzsch G, Lehr E, Ducotterd J-M, and Müller A. 2005. The Atlas Mountains, not the Strait of Gibraltar, as a biogeographic barrier for Mauremys leprosa (Reptilia: Testudines). Salamandra 41(3):97-106.

Garcia-Diez M, FRAILE BO, and MAESTU IB. 2013. NEANDERTHAL GRAPHIC BEHAVIOR: The Pecked Pebble from Axlor Rockshelter (Northern Spain). Journal of anthropological research 69(3):397-410.

Garralda MD, Tillier A, Vandermeersch B, Cabrera V, and Gambier D. 1992. Restes humains de l'Aurignacien archaïque de la Cueva de El Castillo (Santander, Espagne). Anthropologie (Brno) 3:159-164.

Gibbons A. 2011. A new view of the birth of Homo sapiens. Science 331(6016):392-394.

Godsoe W, and Harmon LJ. 2012. How do species interactions affect species distribution models? Ecography 35(9):811-820.

Golovanova L, Hoffecker JF, Kharitonov V, and Romanova G. 1999. Mezmaiskaya Cave: A Neanderthal Occupation in the Northern Caucasus1. JSTOR. p 77-86.

Golovanova LV, Doronichev VB, Cleghorn NE, Koulkova MA, Sapelko TV, and Shackley MS. 2010. Significance of ecological factors in the Middle to Upper Paleolithic transition. Current Anthropology 51(5):655-691.

González-Urquijo J, Ibáñez JJ, Lazuén T, and Mozota M. 2014. Axlor. In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 45-48.

González Morales MR, and Straus LG. 2014. Cueva del Mirón (Ramales de la Victoria, Cantabria). Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos: Spain. p 110-114.

Grinnell J. 1917. The niche-relationships of the California Thrasher. The Auk 34(4):427-433.

Hammond M. 1982. The expulsion of the Neanderthals from human ancestry: Marcellin Boule and the social context of scientific research. Social Studies of Science 12(1):1-036.

Hardesty DL. 1975. The niche concept: suggestions for its use in human ecology. Human Ecology 3(2):71-85.

Hardesty DL. 1980. The use of general ecological principles in archaeology. Advances in archaeological method and theory 3:157-187.

Hardy BL. 2010. Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. Quaternary Science Reviews 29(5):662-679.

Hardy BL, and Moncel M-H. 2011. Neanderthal use of fish, mammals, birds, starchy plants and wood 125-250,000 Years Ago. PloS one 6(8):e23768.

Harvati K, Frost SR, and McNulty KP. 2004. Neanderthal taxonomy reconsidered: implications of 3D primate models of intra-and interspecific differences. Proceedings of the National Academy of Sciences of the United States of America 101(5):1147-1152.

Harvati K, Panagopoulou E, and Karkanas P. 2003. First Neanderthal remains from Greece: the evidence from Lakonis. Journal of Human Evolution 45(6):465-473.

Heinrich H. 1988. Origin and consequences of cyclic ice rafting in the northeast Atlantic Ocean during the past 130,000 years. Quaternary research 29(2):142-152.

Henry AG, Brooks AS, and Piperno DR. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). Proceedings of the National Academy of Sciences 108(2):486-491.

Hewitt GM. 2001. Speciation, hybrid zones and phylogeography—or seeing genes in space and time. Molecular Ecology 10(3):537-549.

Higham T, Douka K, Wood R, Ramsey CB, Brock F, Basell L, Camps M, Arrizabalaga A, Baena J, and Barroso-Ruíz C. 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512(7514):306-309.

Higham T, Ramsey CB, Karavanić I, Smith FH, and Trinkaus E. 2006. Revised direct radiocarbon dating of the Vindija G1 Upper Paleolithic Neandertals. Proceedings of the National Academy of Sciences of the United States of America 103(3):553-557.

Hirzel A, Hausser J, Chessel D, and Perrin N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83(7):2027-2036.

Hoffecker JF. 2009. Neanderthal and modern human diet in eastern Europe. The Evolution of Hominin Diets: Springer. p 87-98.

Hoffecker JF, and Cleghorn N. 2000. Mousterian hunting patterns in the northwestern Caucasus and the ecology of the Neanderthals. International Journal of Osteoarchaeology 10(5):368-378.

Holliday TW. 2014. Neanderthals and Their Contemporaries. Encyclopedia of Global Archaeology: Springer. p 5170-5182.

Holt RD. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences 106(Supplement 2):19659-19665.

Horan RD, Bulte E, and Shogren JF. 2005. How trade saved humanity from biological exclusion: An economic theory of Neanderthal extinction. Journal of Economic Behavior & Organization 58(1):1-29.

Howell FC. 1951. The place of Neanderthal man in human evolution. American Journal of Physical Anthropology 9(4):379-416.

Howell FC. 1957. The evolutionary significance of variation and varieties of "Neanderthal" man. Quarterly Review of Biology:330-347.

Howells W. 1967. Mankind in the making: the story of human evolution: ICON Group International.

Howells WW. 1942. Fossil man and the origin of races. American Anthropologist 44(2):182-193.

Howells WW. 1976. Explaining modern man: evolutionists versus migrationists. Journal of Human Evolution 5(5):477-495.

Hrdlička A. 1927. The Neanderthal Phase of Man. The Journal of the Royal Anthropological Institute of Great Britain and Ireland 57:249-274.

Hublin J-J. 1978. Le torus occipital transverse et les structures associées: évolution dans le genre Homo.

Hublin J-J. 2001. Northwestern African Middle Pleistocene hominids and their bearing on the emergence of Homo sapiens. Human Roots:99-121.

Hublin J-J. 2009. The origin of Neandertals. Proceedings of the National Academy of Sciences 106(38):16022-16027.

Hublin J-J. 2013. The makers of the early Upper Paleolithic in western Eurasia. The origins of modern humans: biology reconsidered John Wiley & Sons, Inc, New Jersey:223-252.

Hublin J-J, Talamo S, Julien M, David F, Connet N, Bodu P, Vandermeersch B, and Richards MP. 2012. Radiocarbon dates from the Grotte du Renne and Saint-

Césaire support a Neandertal origin for the Châtelperronian. Proceedings of the National Academy of Sciences 109(46):18743-18748.

Hublin J. 1988. Caractères dérivés de la région occipito-mastoïdienne chez les Néandertaliens. L'Anatomie 3:67-73.

Huijzer A, and Isarin R. 1997. The reconstruction of past climates using multi-proxy evidence: an example of the Weichselian Pleniglacial in northwest and central Europe. Quaternary Science Reviews 16(6):513-533.

Hutchinson G. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantative Biology: Cold Spring Harbor Laboratory Press. p 415-427.

Jaramillo-Correa J, Grivet D, Terrab A, Kurt Y, De-Lucas A, Wahid N, Vendramin G, and González-Martínez S. 2010. The Strait of Gibraltar as a major biogeographic barrier in Mediterranean conifers: a comparative phylogeographic survey. Molecular Ecology 19(24):5452-5468.

Jiménez-Valverde A, Peterson AT, Soberón J, Overton J, Aragón P, and Lobo JM. 2011. Use of niche models in invasive species risk assessments. Biological Invasions 13(12):2785-2797.

Jöris O, Fernandez EÁ, and Weninger B. 2003. Radiocarbon evidence of the Middle to Upper Palaeolithic transition in southwestern Europe. Trabajos de prehistoria 60(2):15-38.

Julià R, and Bischoff JL. 1991. Radiometric dating of Quaternary deposits and the hominid mandible of Lake Banyolas, Spain. Journal of Archaeological Science 18(6):707-722.

Kearney M, and Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology letters 12(4):334-350.

Keith A. 1915. The Antiquity of Man. London: Williams and Norgate.

Keith A. 1925. The Antiquity of Man, Vol. II. London: Williams and Norgate.

Keith A. 1931. New discoveries relating to the antiquity of man: WW Norton, Incorporated.

Keith A. 1948. A New Theory of Human Evolution. London: Watts & Co.

Keith A, and McCown TD. 1937. Mount Carmel man: His bearing on the ancestry of modern races. Early Man:41-52.

Klein RG. 2003. Whither the Neanderthals? Science 299(5612):1525-1527.

Kuhn SL. 1995. Mousterian lithic technology: An ecological perspective: Princeton University Press.

Kupka F. 1909. An Ancestor: The Man of Twenty Thousand Years Ago. The Illustrated London News, L'Illustration: The Illustrated London News, L'Illustration.

Leakey LS, Tobias PV, and Napier JR. 1964. A new species of the genus Homo from Olduvai Gorge. Nature 202(4927):7-9.

Leakey LSB. 1961. The progress and evolution of man in Africa: London, Oxford U. P.

Lipman JK. 1934. The Age of Man, II. Thought 9(2):206-221.

Lozier J, Aniello P, and Hickerson M. 2009. Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. Journal of Biogeography 36(9):1623-1627.

MacCurdy G. 1924. Human origins, Vol. 2. New York, Appleton.

Maíllo Fernández JM, Arteaga C, Iriarte-Chiapusso M-J, Fernández A, Wood R, and Bernaldo de Quirós F. 2014. Cueva Morín (Villanueva de Villaescusa, Cantabria). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 72-78.

Maroto Genover J. 1993. La cueva de los Ermitons (Sales de Llierca, Girona): un yacimiento del Paleolítico Medio final.

Maroto J. 1985. Un jaciment prehistòric a l'interior del massís de l'Alta Garrotxa: la Cova dels Ermitons. Vitrina 1:37-48.

Maroto J, Soler N, and Fullola J. 1996. Cultural change between middle and upper Palaeolithic in Catalonia. The last Neandertals, the first anatomically modern humans: a tale about human diversity Cultural change and human evolution: the crisis at 40 Ka BP:219-250.

Maroto J, Vaquero M, Arrizabalaga Á, Baena J, Baquedano E, Jordá J, Julià R, Montes R, Van Der Plicht J, and Rasines P. 2012. Current issues in late Middle Palaeolithic chronology: New assessments from Northern Iberia. Quaternary International 247:15-25.

Martínez-Moreno J, Mora R, and de la Torre I. 2010. The Middle-to-upper Palaeolithic transition in Cova Gran (Catalunya, Spain) and the extinction of Neanderthals in the Iberian peninsula. Journal of Human Evolution 58(3):211-226.

Martínez-Meyer E, Townsend Peterson A, and Hargrove WW. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13(4):305-314.

Mayr E. 1962. Origin of the human races. Science 138(3538):400-422.

McCown TD, and Keith SA. 1939. The Stone Age of Mount Carmel: The Fossil Human Remains from the Levallosiso-Mousterian: Clarendon Press.

McNyset KM, and Blackburn JK. 2006. Does GARP really fail miserably? A response to Stockman et al.(2006). Diversity and Distributions 12(6):782-786.

Menéndez M, Weniger G-C, Álvarez-Alonso D, de Andrés-Herrero M, García E, Jordá J, Kehl M, Rojo J, Quesdada JM, and Schmidh I. 2014. La Cueva de la Güelga. Cangas de Onís. Asturias. In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos: Universidad de Burgos, Fundación Atapuerca. p 60-63.

Menozzi P, Piazza A, and Cavalli-Sforza L. 1978. Synthetic maps of human gene frequencies in Europeans. Science 201(4358):786-792.

Michel V, Delanghe-Sabatier D, Bard E, and Ruiz CB. 2013. U-series, ESR and 14 C studies of the fossil remains from the Mousterian levels of Zafarraya Cave (Spain): A revised chronology of Neandertal presence. Quaternary Geochronology 15:20-33.

Montagu A. 1963. What is remarkable about varieties of man is likenesses, not differences. Current Anthropology 4(4):361-364.

Montagu M. 1947. Comments on Weidenreich's Paper concerning the Origin of Homo Sapiens. American anthropologist 49(4):686-689.

Mora R, Martínez-Moreno J, and Casanova J. 2008. Abordando la noción de "variabilidad musteriense" en Roca dels Bous (Prepirineo suroriental, Lleida). Trabajos de prehistoria 65(2):13-28.

Mora R, Martínez-Moreno J, Gilabert XR, de la Torre I, Benito-Calvo A, Roy M, Samper S, Vega S, Pizarro J, and Plasencia J. 2014. The Mousterian site of Roca dels Bous (Lleida, Pre-pryrenes). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeologicla Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 159-162.

Morant G. 1930. Studies of Palaeolithic man. Annals of Eugenics 4(1-2):109-214.

Nogués-Bravo D. 2009. Predicting the past distribution of species climatic niches. Global Ecology and Biogeography 18(5):521-531.

Oakley KP, and Weiner JS. 1955. Piltdown man. American Scientist 43(4):573-583.

Panagopoulou E, Karkanas P, Tsartsidou G, Kotjabopoulou E, Harvati K, and Ntinou M. 2004. Late Pleistocene archaeological and fossil human evidence from Lakonis cave, southern Greece. Journal of Field Archaeology 29(3-4):323-349.

Pantoja Pérez A, Sala Burgos M, García García N, Ruiz Zapata MB, García G, José M, Aranburu A, Arsuaga JL, and Casabó i Bernard J. 2011. Análisis paleontológico del yacimiento del Pleistoceno superior de Cova Foradada (Xàbia, Alicante, España). Boletín de la Real Sociedad Española de Historia Natural Sección geológica 105(1-4):53-66.

Pastoors A, and Tafelmaier Y. 2012. What about flakes? Flake production and core reduction strategies in the Aurignacian of the Rhineland: Lommersum IIc (North Rhine Westphalia) and Wildscheuer III (Hessen). A Pastoors & M Peresani (Hg) Flakes not blades: the role of flake production at the onset of the Upper Palaeolithic in Europe Wissenschaftliche Schriften des Neanderthal Museums 5:165-180.

Pearson R, Dawson T, Berry P, and Harrison P. 2002. SPECIES: a spatial evaluation of climate impact on the envelope of species. Ecological modelling 154(3):289-300.

Pearson RG, Dawson TP, and Liu C. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27(3):285-298.

Pearson RG, Raxworthy CJ, Nakamura M, and Townsend Peterson A. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34(1):102-117.

Peresani M. 2008. A new cultural frontier for the last Neanderthals: the Uluzzian in Northern Italy. Current Anthropology 49(4):725-731.

Peterson AT. 2011. Ecological niche conservatism: A time-structured review of evidence. Journal of Biogeography 38(5):817-827.

Peterson AT, and Cohoon KP. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological modelling 117(1):159-164.

Peterson AT, and Martínez-Meyer E. 2007. Geographic evaluation of conservation status of African forest squirrels (Sciuridae) considering land use change and climate

change: the importance of point data. Biodiversity and conservation 16(14):3939-3950.

Peterson AT, and Nyari AS. 2008. Ecological Niche Conservatism and Pleistocene Refugia in the Trush-like Mourner, *Schiffornis* sp., in the Neotropics. Evolution 62(1):173-183.

Peterson AT, Papeş M, and Soberón J. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological modelling 213(1):63-72.

Peterson AT, and Vieglais DA. 2001. Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack a Pressing Problem: A new approach to ecological niche modeling, based on new tools drawn from biodiversity informatics, is applied to the challenge of predicting potential species' invasions. BioScience 51(5):363-371.

Pettitt P. 2011. The Palaeolithic origins of human burial: Routledge.

Phillips SJ, and Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2):161-175.

Pike-Tay A, Cabrera Valdés V, and Bernaldo de Quirós F. 1999. Seasonal variations of the Middle–Upper Paleolithic transition at El Castillo, Cueva Morın and El Pendo (Cantabria, Spain). Journal of Human Evolution 36(3):283-317.

Pinto Llona AC. 2014. 25,000 years of Palaeolithic occupation at Sopeña (Asturias, Spain). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca. p 129-132.

Qiao H, Soberón J, and Peterson AT. 2015. No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. Methods in Ecology and Evolution 6(10):1126-1136.

Relethford J. 2008. Genetic evidence and the modern human origins debate. Heredity 100(6):555-563.

Relethford JH. 1998. Genetics of modern human origins and diversity. Annual Review of Anthropology:1-23.

Relethford JH. 2001. Absence of regional affinities of Neandertal DNA with living humans does not reject multiregional evolution. American journal of physical anthropology 115(1):95-98.

Richards MP, and Trinkaus E. 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. Proceedings of the National Academy of Sciences 106(38):16034-16039.

Riel-Salvatore J. 2009. What is a 'transitional'industry? The Uluzzian of southern Italy as a case study. Sourcebook of Paleolithic transitions: Springer. p 377-396.

Riel-Salvatore J. 2010. A niche construction perspective on the Middle–Upper Paleolithic transition in Italy. Journal of archaeological method and theory 17(4):323-355.

Rink W, Schwarcz H, Lee H, Valdés VC, De Quirós FB, and Hoyos M. 1996. ESR dating of tooth enamel: comparison with AMS 14 C at El Castillo Cave, Spain. Journal of Archaeological Science 23(6):945-951.

Romanillo JM, and Soto EG. 1983. Radiocarbon Dating of the Mousterian at Cueva Millan (Hortiguela, Burgos, Spain). Current Anthropology 24(2):232-233.

Rots V. 2009. The functional analysis of the Mousterian and Micoquian assemblages of Sesselfelsgrotte, Germany: aspects of tool use and hafting in the European Late Middle Palaeolithic. Quartar 56:37-66.

Rougier H, Milota Ş, Rodrigo R, Gherase M, Sarcină L, Moldovan O, Zilhão J, Constantin S, Franciscus RG, and Zollikofer CP. 2007. Peştera cu Oase 2 and the cranial morphology of early modern Europeans. Proceedings of the National Academy of Sciences 104(4):1165-1170.

Santa Luca A. 1978. A re-examination of presumed Neandertal-like fossils. Journal of Human Evolution 7(7):619-636.

Santamaria D, Duarte E, González-Pumariega M, Martínez L, Suárez P, Fernández de la Vega J, Santos G, Higham T, Wood R, and de la Rasilla M. 2014. La Viña rock shelter (Asturias, Spain). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. p 95-99.

Schmitt D, Churchill SE, and Hylander WL. 2003. Experimental evidence concerning spear use in Neandertals and early modern humans. Journal of Archaeological Science 30(1):103-114.

Schmitz RW, Serre D, Bonani G, Feine S, Hillgruber F, Krainitzki H, Pääbo S, and Smith FH. 2002. The Neandertal type site revisited: interdisciplinary investigations of skeletal remains from the Neander Valley, Germany. Proceedings of the National Academy of Sciences 99(20):13342-13347.

Schwarcz H, Grün R, Vandermeersch B, Bar-Yosef O, Valladas H, and Tchernov E. 1988. ESR dates for the hominid burial site of Qafzeh in Israel. Journal of Human Evolution 17(8):733-737.

Shaw CN, and Stock JT. 2013. Extreme mobility in the Late Pleistocene? Comparing limb biomechanics among fossil Homo, varsity athletes and Holocene foragers. Journal of human evolution 64(4):242-249.

Shipman P. 2008. Separating "us" from "them": Neanderthal and modern human behavior. Proceedings of the National Academy of Sciences 105(38):14241-14242.

Skinner A, Blackwell B, Martin S, Ortega A, Blickstein J, Golovanova L, and Doronichev V. 2005. ESR dating at Mezmaiskaya Cave, Russia. Applied radiation and isotopes 62(2):219-224.

Smith FH, Falsetti AB, and Donnelly SM. 1989. Modern human origins. American Journal of Physical Anthropology 32(S10):35-68.

Smith FH, Hutchinson VT, and Janković I. 2012. Assimilation and modern human origins in the African peripheries. African Genesis: Perspectives on Hominin Evolution 62:365.

Smith TM, Toussaint M, Reid DJ, Olejniczak AJ, and Hublin J-J. 2007. Rapid dental development in a middle Paleolithic Belgian Neanderthal. Proceedings of the National Academy of Sciences 104(51):20220-20225.

Soberón J, and Peterson AT. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1-10.

Sondaar P, Elhurg R, Holmeijer GK, Martini F, Sanges M, Spaan A, and de Visser H. 1995. The human colonization 0f Sardinia: a Late—Pleisœcene human fossil from Corbeddu cave.

Soressi M. 2005. Late Mousterian lithic technology: its implications for the pace of the emergence of behavioural modernity and the relationship between behavioural modernity and biological modernity. From tools to symbols:389-417.

Spencer F, and Smith FH. 1981. The significance of Aleš Hrdlička's "Neanderthal phase of man": A historical and current assessment. American journal of physical anthropology 56(4):435-459.

Stewart T. 1964. A neglected primitive feature of the Swanscombe skull. The Swanscombe Skull, A Survey of Research on a Pleistocene Site, Roy Anthrop Inst of Great Britain and Ireland, Londres:151-159.

Stockman AK, Beamer DA, and Bond JE. 2006. An evaluation of a GARP model as an approach to predicting the spatial distribution of non-vagile invertebrate species. Diversity and Distributions 12(1):81-89.

Stockwell D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International journal of geographical information science 13(2):143-158.

Stockwell D, and Peterson AT. 2002a. Controlling bias in biodiversity data. Predicting species occurrences: issues of accuracy and scale Island Press, Washington, DC:537-546.

Stockwell DR, and Peterson AT. 2002b. Effects of sample size on accuracy of species distribution models. Ecological modelling 148(1):1-13.

Stringer C. 2014. Why we are not all multiregionalists now. Trends in ecology & evolution 29(5):248-251.

Stringer C, and Andrews P. 1988. The origin of modern humans. Science 239:1263-1268.

Stringer C, Finlayson J, Barton R, Fernández-Jalvo Y, Cáceres I, Sabin R, Rhodes E, Currant A, Rodríguez-Vidal J, and Giles-Pacheco F. 2008. Neanderthal exploitation of marine mammals in Gibraltar. Proceedings of the National Academy of Sciences 105(38):14319-14324.

Stringer C, and Hublin J-J. 1999. New age estimates for the Swanscombe hominid, and their significance for human evolution. Journal of Human Evolution 37(6):873-877.

Stringer CB. 1992. Replacement, continuity and the origin of Homo sapiens. Continuity or replacement:9-24.

Stringer CB, Grün R, Schwarcz H, and Goldberg P. 1989. ESR dates for the hominid burial site of Es Skhul in Israel. Nature 338(6218):756-758.

Sutton T, De Giovanni R, and Siqueira MF. 2007. Introducing Open Modeller-A fundamental niche modelling framework. OSGeo Journal 1(1).

Tchernov E. 2002. The faunal sequence of the southwest Asian Middle Paleolithic in relation to hominid dispersal events. Neandertals and modern humans in western Asia: Springer. p 77-94.

Templeton AR. 2007. Genetics and recent human evolution. Evolution 61(7):1507-1519.

Terberger T, and Street M. 2003. New evidence for the chronology of the Aurignacian and the question of Pleniglacial settlement in western central Europe. The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Stratigraphies, Cultural Implications, Trabalhos de Arqueologia 33:213-221.

Thorne AG, and Wolpoff MH. 1981. Regional continuity in Australasian Pleistocene hominid evolution. American Journal of Physical Anthropology 55(3):337-349.

Tilney F. 1927. The brain of prehistoric man: A study of the psychologic foundations of human progress. Archives of Neurology & Psychiatry 17(6):723-769.

Tortosa JEA, Bonilla VV, Ripoll MP, Valle RM, and Calatayud PG. 2002. Big game and small prey: Paleolithic and Epipaleolithic economy from Valencia (Spain). Journal of Archaeological Method and Theory 9(3):215-268.

Townsend Peterson A, Papeş M, and Eaton M. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30(4):550-560.

Trinkaus E. 1986. The Neandertals and modern human origins. Annual Review of Anthropology:193-218.

Trinkaus E. 1993. Femoral neck-shaft angles of the Qafzeh-Skhul early modern humans, and activity levels among immature Near Eastern Middle Paleolithic hominids. Journal of Human Evolution 25(5):393-416.

Trinkaus E. 2005. Early modern humans. Annu Rev Anthropol 34:207-230.

Trinkaus E. 2007. European early modern humans and the fate of the Neandertals. Proceedings of the National Academy of Sciences 104(18):7367-7372.

Trinkaus E. 2011. Late Neandertals and Early Modern Humans in Europe, Population Dynamics and Paleobiology. Continuity and discontinuity in the peopling of Europe: Springer. p 315-329.

Trinkaus E, Maki J, and Zilhão J. 2007. Middle Paleolithic human remains from the Gruta da Oliveira (Torres Novas), Portugal. American journal of physical anthropology 134(2):263-273.

Trinkaus E, Moldovan O, Bîlgăr A, Sarcina L, Athreya S, Bailey SE, Rodrigo R, Mircea G, Higham T, and Ramsey CB. 2003. An early modern human from the Peştera cu Oase, Romania. Proceedings of the National Academy of Sciences 100(20):11231-11236.

Trinkaus E, and Shipman P. 1993. The Neandertals: Changing the image of mankind: Alfred a Knopf Inc.

Turu V, Calvet M, Bordonau J, Gunnell Y, Delmas M, Vilaplana JM, and Jalut G. 2016. Did Pyrenean glaciers dance to the beat of global climatic events? Evidence from the Würmian sequence stratigraphy of an ice-dammed palaeolake depocentre in Andorra. Geological Society, London, Special Publications 433:SP433. 436.

Valladas H, Mercier N, Joron JL, McPherron SP, Dibble HL, and Lenoir M. 2003. TL dates for the middle paleolithic site of Combe-Capelle Bas, France. Journal of Archaeological Science 30(11):1443-1450.

Valladas H, Reyss J-L, Joron J-L, Valladas G, Bar-Yosef O, and Vandermeersch B. 1988. Thermoluminescence dating of Mousterian Troto-Cro-Magnon'remains from Israel and the origin of modern man. Nature 331(6157):614-616.

Vallois HV. 1954. Neandertals and praesapiens. The Journal of the Royal Anthropological Institute of Great Britain and Ireland 84(1/2):111-130.

Vallois HV. 1958. La grotte de Fontéchevade Paris: Masson. 263 p.

Vallverdú J, Allué E, Bargalló A, Cáceres I, Campeny G, Chacón MG, Gabucio MJ, Gómez B, López-García JM, Fernández M et al. . 2014. Abric Romaní (Capellades, Anoia). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos, Fundación Atapuerca.

Van Andel TH, and Tzedakis PC. 1996. Palaeolithic landscapes of Europe and environs, 150,000-25,000 years ago: an overview. Quaternary Science Reviews 15(5):481-500.

Vaquero M, Allué E, Bischoff JL, Burjachs F, and Vallverdú J. 2013. Environmental, depositional and cultural changes in the Upper Pleistocene and early Holocene: the Cinglera del Capelló sequence (Capellades, Spain). Quaternaire Revue de l'Association française pour l'étude du Quaternaire 24(1):49-64.

Vaquero M, Maroto J, Arrizabalaga A, Baena J, Baquedano E, Carrión E, Jorda J, Martinón M, Menéndez M, and Montes R. 2006a. The Neandertal-Modern Human meeting in Iberia: a critical view of the cultural, geographical and chronological data. When Neanderthals and Modern Human Meets Kerns Verlag, Tübingen:419-441.

Vaquero M, Maroto J, Arrizabalaga Á, Baena J, Baquedano E, Carrión E, Jordá J, Martinón M, Menéndez M, and Rosell J. 2006b. When Neanderthals and Modern Humans Met. In: Conard N, editor. The Neanderthal-modern human meeting in

Iberia: a critical view on the cultural, geogrpahical, and chronological data. Kerns Verlag, Tübingen. p 419-439.

Varela S, Lobo JM, and Hortal J. 2011. Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. Palaeogeography, Palaeoclimatology, Palaeoecology 310(3):451-463.

Vega G, Raposo L, and Santonja M. 1999. Environments and settlement in the Middle Palaeolithic of the Iberian Peninsula. The middle palaeolithic occupation of Europe:23-48.

Villaverde V, and Fumanal MP. 1990. Relations entre le Paléolithique moyen et le Paléolithique supérieur dans le versant méditerranéen espagnol. Paléolithique moyen récent et Paléolitique superieur ancien en Europe, Mémoires du Musée de Préhist d'île-de-France 3:177-183.

Walker M, López-Martínez M, and Haber-Uriarte M. 2014. Sima de las Palomas del Cabezo Gordo (Torre Pacheco, Murcia, Spain). In: Ramos RS, editor. Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait: The Current Archaeological Record. Burgos, Spain: Universidad de Burgos
Fundación Atapuerca. p 410-413.

Walker MJ, Gibert J, López MV, Lombardi AV, Pérez-Pérez A, Zapata J, Ortega J, Higham T, Pike A, and Schwenninger J-L. 2008. Late Neandertals in Southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. Proceedings of the National Academy of Sciences 105(52):20631-20636.

Waltari E, and Guralnick RP. 2009. Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. Journal of Biogeography 36(1):148-161.

Washburn SL. 1964. The Origin of Races: Weidenreich's Opinion. American Anthropologist 66(5):1165-1167.

Weidenreich F. 1940. Some problems dealing with ancient man. American Anthropologist 42(3):375-383.

Weidenreich F. 1941. The brain and its role in the phylogenetic transformation of the human skull. Transactions of the American Philosophical Society 31(5):320-442.

Weidenreich F. 1943a. The "Neanderthal man" and the ancestors of "Homo sapiens". American Anthropologist 45(1):39-48.

Weidenreich F. 1943b. The Skull of Sinanthropus pekinensis; a comparative study on a primitive hominid skull. Lancaster: Lancaster Press.

Weidenreich F. 1945. The Keilor skull: a Wadjak type from southeast Australia. American Journal of Physical Anthropology 3(1):21-32.

Weidenreich F. 1946. Generic, specific and subspecific characters in human evolution. American journal of physical anthropology 4(4):413-432.

Weidenreich F. 1947a. Facts and speculations concerning the origin of Homo sapiens. American Anthropologist 49(2):187-203.

Weidenreich F. 1947b. The trend of human evolution. Evolution:221-236.

Weiner J, and Oakley K. 1954. The Piltdown fraud: available evidence reviewed. American journal of physical anthropology 12(1):1-8.

Weiner JS, Oakley KP, and Le Gros Clark W. 1953. The solution of the Piltdown problem. Bulletin of the British Museum (Natural History), Geology 2(3):139-146.

Weninger B, Danzeglocke U, and Jöris O. 2005. Comparison of dating results achieved using different radiocarbon-age calibration curves and data. Unpublished manuscript.

Willman JC, Maki J, Bayle P, Trinkaus E, and Zilhão J. 2012. Middle Paleolithic Human Remains from the Gruta da Oliveira (Torres Novas), Portugal. American journal of physical anthropology 149(1):39-51.

Wolpoff M. 1989. Early "Modern" Humans from the Levant? The Problem of Adaptation. American Association of Physical Anthropology 78(2):326.

Wolpoff M, Mannheim B, Mann A, Hawks J, Caspari R, Rosenberg K, Frayer D, Gill G, and Clark G. 2004. Why not the Neandertals? World Archaeology 36(4):527-546.

Wolpoff MH. 1984. Evolution in Homo erectus: the question of statis. Paleobiology:389-406.

Wolpoff MH, Hawks J, and Caspari R. 2000. Multiregional, not multiple origins.

Wolpoff MH, Hawks J, Frayer DW, and Hunley K. 2001. Modern human ancestry at the peripheries: a test of the replacement theory. Science 291(5502):293-297.

Wolpoff MH, Wu X, and Thorne AG. 1984. Modern Homo sapiens origins: a general theory of hominid evolution involving the fossil evidence from East Asia. The origins of modern humans: a world survey of the fossil evidence 6:411-483.

Wood R, Arrizabalaga A, Camps M, Fallon S, Iriarte-Chiapusso M-J, Jones R, Maroto J, De La Rasilla M, Santamaría D, and Soler J. 2014. The chronology of the earliest Upper Palaeolithic in northern Iberia: New insights from L'Arbreda, Labeko Koba and La Viña. Journal of human evolution 69:91-109.

Wood RE, Barroso-Ruíz C, Caparrós M, Pardo JFJ, Santos BG, and Higham TF. 2013. Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. Proceedings of the National Academy of Sciences 110(8):2781-2786.

Zilhao J. 1997. The Ebro frontier and the extinction of Neandertals. Journal of Human Evolution: ACADEMIC PRESS LTD 24-28 OVAL RD, LONDON, ENGLAND NW1 7DX. p A25-A26.

Zilhao J. 2006. Chronostratigraphy of the Middle-to-Upper Paleolithic transition in the Iberian Peninsula. Pyrenae(37):7-84.

Zilhão J. 1998. The extinction of Iberian Neandertals and its implications for the origins of modern humans in Europe. XIII international congress of prehistoric and protohistoric sciences Proceedings. p 299-312.

Zilhão J. 2000. The Ebro frontier: a model for the late extinction of Iberian Neanderthals. Neanderthals on the Edge Oxbow Books, Oxford:111-121.

Zilhão J. 2001. Neandertal/modern human interaction in Europe. BAR INTERNATIONAL SERIES 1005:13-20.

Zilhão J. 2009. The Ebro frontier revisited. The Mediterranean from 50(000):293-312.

Zilhão J, Banks WE, d'Errico F, and Gioia P. 2015. Analysis of site formation and assemblage integrity does not support attribution of the Uluzzian to modern humans at Grotta del Cavallo. PloS one 10(7):e0131181.

Zilhão J, and d'Errico F. 1999. The chronology and taphonomy of the earliest Aurignacian and its implications for the understanding of Neandertal extinction. Journal of world prehistory 13(1):1-68.

Zilhão J, d'Errico F, Bordes J-G, Lenoble A, Texier J-P, and Rigaud J-P. 2006. Analysis of Aurignacian interstratification at the Châtelperronian-type site and implications for the behavioral modernity of Neandertals. Proceedings of the National Academy of Sciences 103(33):12643-12648.

Zilhão J, and Pettitt P. 2006. On the new dates for Gorham's Cave and the late survival of Iberian Neanderthals. Before Farming 3(3):1-9.

Zilhão J, Trinkaus E, Constantin S, Milota Ş, Gherase M, Sarcina L, Danciu A, Rougier H, Quilès J, and Rodrigo R. 2007. The Peştera cu Oase people, Europe's earliest modern humans. Rethinking the human revolution:249-262.